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MOVEMENTS AND BREEDING BIOLOGY OF BLUE GROUSE IN RELATION TO RECRUITMENT, REPRODUCTIVE SUCCESS, AND MIGRATION.

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LENNART G. SOPUCK

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled MOVEMENTS AND BREEDING BIOLOGY OF BLUE GROUSE IN RELATION TO RECRUITMENT, REPRODUCTIVE SUCCESS, AND MIGRATION. submitted by LENNART G. SOPUCK
in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE

ABSTRACT

Movements of yearling and adult female, and yearling male blue grouse (Dendragapus obscurus fuliginosus) were studied in spring and summer, 1976 and 1977, on Vancouver Island, British Columbia. Movements of yearlings during the period of spring recruitment were emphasized.

Most yearlings recorded on the study area entered the breeding population. About 46% of radio-marked yearlings localized soon after arrival on breeding range, while 54% moved widely well into the recruitment period. Seventeen percent of potential yearling recruits entered sub-optimal habitat. By contrast, all adult females established on prime habitat.

Yearling females moved more widely and localized later in their reproductive cycles and nested later in the breeding season than adult females. Many yearlings may have been delayed in nesting by established hens. Yearling males did not appear to breed, but most showed prolonged site attachment. They generally returned to this area of site attachment as territorial adults the following year.

Radio-tagged hens hatched 47% of their clutches. Because of renesting, 52% of nesting females were successful. Fate of nests of radio-tagged hens was independent of overhead concealment, although a larger sample from earlier years on the same area showed that nests with most cover were most successful. Predators hunting by smell and sight accounted for most egg predation. Nesting

success was independent of time of nest initiation, age of the hen, and extent of movement prior to nesting. Yearlings that entered sub-optimal habitat had low nesting success and brood survival.

Renesting was more frequent among adult than yearling females. Hens initiated second clutches about 13 days after losing their first and most remained on their pre-nesting home ranges. The renesting interval depended on the stage of nesting at which loss occurred. The proportion of females renesting may explain yearly variations in production.

Hens with broods moved widely during the first 2 weeks after hatching and then gradually expanded their ranges at varying distances from their nests. Hens without broods also travelled widely after losing clutches or young chicks, but eventually restricted their movements and then gradually expanded their ranges. Considerable variation in the sizes of home ranges of brood and broodless hens existed.

Broodless hens and yearling males were more secretive in their behaviour, selected denser cover, and migrated earlier than brood hens and adult males, respectively. Migration to winter range was initiated by sudden movements into upland coniferous forests to the west or southwest. Locations of permanent wintering areas were not determined, although directions of travel indicated that widely separated areas were utilized.

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Crown Zellerbach of Canada, Ltd. Courtenay Division, kindly allowed access to their lands.

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INTRODUCTION

Several studies have shown that territorial behaviour may limit the density of avian populations (Brown 1969). Bendell *et al.* (1972) and Zwickel (1972) postulated that the exclusion of yearlings of both sexes was the proximate mechanism limiting recruitment to populations of blue grouse. However, the fates of yearlings so excluded have not been determined. Potential yearling recruits were followed to determine their breeding status and patterns of movement. Movements of adult females were also monitored and this information as well as data on movements of adult males were available for comparison. Although following birds during spring recruitment was the prime objective, movements of hens with and without broods as well as the summer movements of yearling males were described. Monitoring ended with an opportunity to document migration from breeding range.

Two papers are presented in the main body of the thesis:

1. Recruitment of yearlings into a population of blue grouse in spring.
2. Movements and migration of blue grouse after the nesting period.

The first paper is the major work, emphasizing the differences in the ability of yearlings to enter the population, as reflected by their patterns of movement relative to adults. The second paper documents movements of hens with and without broods and the movements of yearling

males after peak breeding. A comparison is made between brood and broodless hens and between adult and yearling males. Finally, the early stages of migration from breeding range are described.

Two shorter works, presented as appendices to this thesis, examine breeding success of radio-tagged hens, factors determining the fates of nests, and renesting in adult and yearling hens. They are entitled:

1. Breeding success and nest predation in blue grouse.
2. Renesting by adult and yearling blue grouse.

PAPER 1. Recruitment of Yearlings into a Population of Blue Grouse in Spring

Abstract

Movements of year old and older blue grouse (*Dendragapus obscurus fuliginosus*) were monitored by radio-telemetry during the spring and summer, 1976 and 1977, on east-central Vancouver Island. Movements of yearlings of both sexes during spring recruitment were emphasized.

Most yearlings entered the breeding population. Survival was high, most females nested, and most males showed prolonged site attachment. About 46% of radio-marked yearlings localized soon after their arrival on breeding range, while 54% tended to move widely well into the recruitment period. Seventeen percent of potential recruits entered sub-optimal habitat. By contrast, all adult females established on prime habitat.

Adult females occupied smaller pre-nesting home ranges, localized earlier in their reproductive cycle, and nested earlier in the breeding season than yearling hens. Many yearling females moved widely and were delayed in nesting, perhaps by established hens.

Recruitment of yearling males coincided with the end of peak breeding. Once they showed prolonged site attachment, they generally returned near to this area as territorial adults. Young males may be driven from territories of adults, but the extent of interaction among themselves or other birds is not known.

Factors causing variation in spring movements of potential recruits relative to adults and their importance in explaining how recruitment is determined are discussed.

Introduction

Established populations of blue grouse on Vancouver Island exhibit relative stability despite marked variation in productivity and constant adult death rates (Zwickel and Bendell 1972; Redfield 1975; Zwickel *et al*. 1977). Many more young are available for recruitment in spring than are necessary to maintain stability. The proximate mechanism limiting recruitment may be exclusion of *surplus* yearlings of both sexes by established residents (Bendell *et al*. 1972; Zwickel 1972).

Surplus birds are usually defined as non-breeders (Brown 1969; Klomp 1972). They may suffer high mortality as Jenkins *et al*. (1963)found with red grouse (*Lagopus lagopus scoticus*). Hannon (1978) provided some evidence that many yearling female blue grouse were non-breeders. Surplus young that do not enter the population seem to disappear from study areas some time in spring, but there is no direct evidence concerning their fates or breeding status.

The primary objective of this study was to determine the fates of potential recruits. The approach was to monitor the movements of yearlings of both sexes during spring and early summer. To see whether yearlings differed in their ability to enter the population, I examined time of recruitment and movements prior to recruitment. Once established, almost all males and females return, in subsequent years, to areas to which they were recruited (Bendell and Elliott 1967). Thus, movement patterns of adult

and yearling grouse were compared to see if those of experienced birds differed from those of birds attempting to enter the population.

Study Areas, Methods and Terminology

Blue grouse were captured on a 1200-ha area in the foothills of east-central Vancouver Island, about 14 km west of Courtenay, British Columbia. This area encompassed Comox Burn and the buffer areas of Zwickel (1977). As some birds dispersed from the capture area, the study area was expanded.

Movements of 46 yearling females, 30 yearling males, and 13 adult females were monitored by radio-telemetry in spring and summer, 1976 and 1977. Observations of banded, but non-radio-tagged adult males, were available for comparison as a result of earlier and concurrent studies. Grouse were radio-tagged in April and early May of each year, less than 3 weeks after arrival on lowland breeding range. Their movements and fates were monitored for 2 to 3 months, the approximate life-span of the radio-packages. This spanned the period of spring recruitment.

The capture area was block-logged between 1947 and 1967 and about 75% was burned by wildfire in 1961. Replanting with Douglas fir (*Pseudotsuga menziesii*) was completed by 1969. In 1976, regrowth varied from 15 years of age at lower elevations (200-400 m) to 7 years at higher elevations (450-650 m). Vegetative structure varied from *dense* in lower areas to *open* or *very open* (Bendell and Elliott 1967) at higher elevations. The capture area is bounded on 3 sides by *very dense* (Bendell and Elliott 1967) vegetation. To the south and east, at elevations below 200 m, *very dense* fir

plantations or alder (*Alnus rubra*) bottoms predominate. To the west, logging ends abruptly as the land rises sharply to form a rolling plateau averaging 1200 m in elevation. Here, undisturbed mature forest predominates. To the northeast, recently logged habitat extends for over 25 km in about a 3-4 km wide zone.

Spring density of blue grouse on Comox Burn, which comprises the lower half of the capture area, was about 20 adult males/km² in 1976 and 1977 (Zwickel *et al.* 1977). The buffer area was censused in 1975 and had a similar density. Numbers have been stable since 1972 (Zwickel *et al.* 1977). Mature forest and dense second growth adjacent to the capture area were not censused, but other studies indicate that this type of habitat supports low numbers of blue grouse (Bendell and Elliott 1966; Redfield *et al.* 1970). Casual observations during my study also suggest that populations were low there. I considered these areas sub-optimal habitat and areas logged and/or burned less than 20 years ago were considered prime habitat.

All yearlings (10-14 months of age), also termed *young* in this paper, were considered *potential recruits* because they were attempting to enter the population for the first time. The *fate* of a potential recruit is defined as its status in the breeding population on the capture area, after recruitment is complete. Recruitment was considered complete for yearling hens by mid-June, beyond the latest possible time for nest initiation and for yearling males by late

June, when migration to winter range by this segment of the population is underway (Sopuck 1978).

Sizes of home ranges of females and yearling males were determined using a modification of the method described by Harvey and Barbour (1965); only peripheral locations less than 1/2 the distance between the 2 most widely separated locations were included.

Radio-transmitters were attached as "back-pack" units (Herzog 1977). The complete package weighed 16-22 g (1-3% of body weight). Birds were equipped with transmitters and released at point of capture within 1 hour. The majority of radio-locations were made with portable telemetry gear, with grouse approached on foot to about 10 m or less and sighted.

Except where specified, chi-square tests for independence or Student's t-tests, were used in statistical analyses. Mean values are presented plus or minus one standard deviation.

Results

On average, birds were located every 5.5 days in 1976 and every 2.5 days in 1977. In both years, movements of females were monitored at least up to start of incubation, if they nested, and movements of most males up to migration to winter range. Movements of yearling males were monitored for an average of 63±21 days (range: 26-112) and a mean number of 20±9.7 locations (range: 6-38) were obtained for each male. Movements of yearling and adult females were followed for an average of 79±28 days (range: 29-132) during the spring and summer. During the important pre-laying period, movements of hens were monitored for an average of 27±10 days (range: 8-56) and a mean number of 10±5.7 locations (range: 3-26) were obtained for each bird.

The 1977 breeding season was advanced relative to 1976. Median date of mating for all females in 1977 (5 May) was different (Median test, $p<.05$) than in 1976 (9 May). Using the combined sample, 77% of the yearling males, 78% of the yearling females, and 100% of the adult females were radio-tagged pricr to peak mating.

Indicators of Recruitment

The prime indicator of recruitment among females was nest initiation. However, nest failures during laying or early incubation may have resulted in some nests not being found. In 2 cases, presence of a brood patch was used as an indicator of recruitment. In 3 cases, where a hen could not

be recaptured, site attachment during the normal period of nest initiation was used to indicate recruitment.

Assessment of recruitment among young males was more difficult. They were secretive and rarely seen in display. Since most do not hold territories (Bendell and Elliott 1967) and because matings are seldom seen, the only absolute measure of recruitment is to observe them on a territory as adults, in subsequent years. This was possible for only 11 of 30 males. Rather, a prolonged period of site attachment was assumed to indicate recruitment. Banding data (F.C. Zwickel, unpublished data) and radio-marking of yearling males support this assumption. The average distance from where 18 non-radio-tagged males were banded as yearlings to where they settled as territorial adults was 506±388 m. The average distance from the centre of areas of site attachment of 11 radio-tagged yearling males to centres of their subsequent adult territories was 605±531 m. These averages were not different ($p>.05$). Combining radio-tagged and non-radio-tagged samples, most males (23/28) returned, as territorial adults, to within 1 km of their banding locations or areas of site attachment as yearlings. Hence, site attachment seems a good indicator of recruitment.

Fates of Potential Recruits and Adult Hens

Recruitment into all habitats

Most radio-tagged yearlings (91%) in my sample apparently entered the population (Table 1). For young

hens, 38 nests were found and 5 others showed evidence of nesting. For young males, 25 showed prolonged site attachment, indicating probable recruitment.

Seven yearlings (9%) did not recruit. Five of these moved widely during the entire recruitment period, including 2 hens that did not nest and 2 males that were killed by predators. Two others, a male and a female, were preyed upon while moving widely, but before the end of the nesting period. As previously mentioned, no nests were found for 3 hens that appeared to localize during the nest initiation period. If these hens did not breed, then a total of 10 yearlings (6 females and 4 males) or 13% of the sample of yearlings did not enter the population. If the 4 birds that were killed by predators are omitted, then only 4-8% of the sample can be considered surplus.

All radio-tagged adult hens bred, with 12 nests found. One adult hen was killed by a predator, but yolk present on the carcass indicated laying was in progress.

Recruitment into sub-optimal habitat

Thirteen of 75 yearlings entered sub-optimal areas after capture on prime habitat (Table 1). The distributions of prime and sub-optimal habitats and movements of yearlings from capture sites to areas of localization in sub-optimal habitats are shown in Figure 1. Six of the hens nested and 5 of the males showed site

attachment and were considered established in dense second growth or mature timber. One hen failed to nest and one male wandered widely; neither was considered to have entered the population. Only one of six hens raised a brood.

If yearlings which did not establish on prime habitat and those that entered sub-optimal habitat are combined, 24% of potential recruits did not enter the population on prime habitat . All adult females nested on prime habitat.

Movement Patterns of Potential Recruits

Movements of radio-tagged grouse were summarized by classifying birds that exhibited site attachment soon after capture and within 1 km of their capture site as "localized" and those that did not exhibit early site attachment as "wide-moving". Figure 2 shows the pre-nesting movements of 3 hens captured before 26 April and more than 25 days before nesting (DBN). They are typical examples of the 3 major patterns of female movements: localized young, localized adults, and wide-moving young. The movements of 3 young males are shown in Figure 3, representing localized and wide-moving patterns of movement.

The proportion of wide-moving and localized patterns of movement among yearlings was about equal (Table 2). Since movements of grouse before capture are unknown, the proportion of wide-moving birds is likely underestimated.

Therefore, at least 1/2 of the potential recruits moved widely during the recruitment period.

This method of estimating the extent of movement of yearlings and adults may simply reflect the time of year the birds were captured. Grouse that were captured soon after migration onto breeding range may tend to move widely, while those captured later in spring may show a greater tendency to localize. However, there was only a weakly significant correlation between date of capture and the straight-line distance to the nest site at time of capture for yearling hens whose nest sites were found ($r=-.39$, Figure 4). Hence, only 15% of the variation in yearling movements can be explained by the date of capture. Furthermore, two yearling hens captured early in spring (before 12 April) and showed displacements of over 2900m still showed, on 1 May, a displacement of over 2000m to their subsequent nest site. Similiarly, only 5% of the variation in the movements of adult hens could be explained by date of capture ($r=-.22$, Figure 5). The relationship between the point of capture and the straight-line distance to the subsequent area of site attachment at time of capture was examined for yearling males. Again, only 7% of the variation in movements could be explained by date of capture ($r=-.27$, Figure 6).

The proportion of each movement type for young hens was different than that of adult hens ($p<.05$); movements of adult hens were mostly of the localized type. Yearlings also had larger pre-nesting home ranges than adults, 12.0±8.8 ha

(n=27) versus 4.6±2.7 ha, (n=10, $p<.02$). A difference between young and adults is also shown by the total distance travelled from 20 DBN (days before nesting) to incubation; yearling hens travelled farther than adults, 2829±1718 m versus 1426 ±494 m ($p<.01$).

Although no adult males were radio-tagged, their movements have been determined by resighting individually marked birds during other studies. Adult males are seldom seen off their territories after their arrival on breeding range in late March. Territories are much smaller than home ranges of yearling males, averaging 0.8 to 4.4 ha in size (from Bendell and Elliott 1967, n=58). Thus, most adult males would almost certainly be considered localized if radio-tagged. By contrast, 43% of young males tended to be wide moving. Several adult territories may be encompassed by the movements of one yearling (Figure 7). On average, for 9 young males whose movements were monitored where territories of adult males were well documented, 4.4±2.6 territories were associated with the movements of each yearling.

Time-specific Movements of Yearling Males and Females

Figures 8 and 9 depict the movements of yearling males and females, respectively, in terms of displacements over specific time periods. Displacement refers to the distance between the first and last location of an individual during a specific period. Small displacements indicate site attachment; large displacements, directional or wide

movements.

In males, wide ranging movements (greater than 800 m) were most prevalent early (Figure 8). As breeding progressed, the proportion of males showing site attachment (less than 800 m) increased to surpass wide-moving males. However, by 18 May to 2 June, when most nests had been initiated, many yearlings were still ranging widely. This figure again shows that yearlings differ in their ability to maintain an area of site attachment, but more accurately depicts the gradient between localized and wide-moving patterns of movement rather than the existence of 2 distinct "groups" as shown in Table 2. The tendency for young males to localize as breeding progressed also was shown by a decrease in size of home ranges as follows: between 16 April and 15 May, average size of home range (28.5±25.2 ha) was larger ($p<.01$) than between 16 May and 15 June (11.9±6.9 ha).

Among yearling females (Figure 9), wide-ranging movements occurred from 40 DBN to 10 DBN, with a peak at about 10 to 20 DBN. By contrast, all displacements during laying were less than 600 m. As with young males, the gradient between localized and wide-moving patterns of movement is evident; the proportion of wide-moving yearling females was greatest 10-20 days prior to laying. The tendency for young hens to localize as breeding progressed, relative to adult hens, was shown by distances to their nest sites at 20 and 10 DBN. For yearlings, the median distances

for 20 and 10 DBN were 705m (N=29) and 240m (N=37), respectively, and for adults, were 240m (N=11) and 205m (N=12), respectively. Yearlings and adults showed an increase in attachment to their nest sites from 20 to 10 DBN, and at both times yearlings showed less site attachment than adults. These differences were significant only at 20 DBN ($p<.05$).

Timing of Recruitment in Yearling Females and Localization for Breeding in Adult Females

I considered localization to occur in females when a grouping of radio-locations occurred where no two locations were greater than 400 m apart. Time of recruitment in yearlings and localization for breeding in adults was defined as when a bird first entered this area of site attachment and remained there to nest.

The median time of recruitment by yearling hens was later than the time of localization for breeding for adult hens (Figure 10 and Median test, $p<.01$). Establishment of adults peaked at about 25 DBN, while recruitment of yearlings had a more asymmetric distribution with a peak at 10-15 DBN. Some yearlings were recruited as early as establishment of adults, but most were delayed until late in their reproductive cycles. Chronologically, most adult hens localized for nesting earlier than yearlings (Figure 11). The average date of localization was significantly earlier for adult hens (18 April) than yearling hens (6 May,

$p<.001$). Also, on average, adults initiated laying of eggs significantly earlier in the breeding season than yearlings (11 May vs 19 May, $p<.001$). These data support the findings of Zwickel (1977) for the period 1969-1975 on Comox Burn. During this period, first hatching of clutches by adults began about 1 week earlier than yearlings.

Timing of Recruitment in Yearling Males

Determination of site attachment and thus timing of recruitment in young males was more difficult than females. However, in most cases there was a cessation of directional movements greater than 800m (from Figure 8), resulting in an area of site attachment. The date when each male first entered this area of site attachment was considered to indicate the approximate time of recruitment.

Most young males were recruited by the end of peak breeding on about 10 May (Figure 12), but ranged from 16 April to 30 May.

Relationship Between Movements of Yearling Males and Territories of Adult Males

Radio-locations (N=185) of 9 yearling males on Comox burn were compared to randomly placed locations (N=75) as to frequency that these locations fell within territories of adult males. Young males were found less frequently than expected on territories if they were travelling at random ($p<.01$). Thus, young males may be avoiding, or are driven

from, territories of adults.

Discussion

Few workers have attempted to follow potential recruits in detail because the fates of animals which "disappear" from an arbitrarily delineated population are difficult to determine. They may have dispersed, died, or remained secretive on the area. Radio-telemetry allows marked animals to be located at will and, providing the initial sample was representative of the cohort in the population, gives a more efficient way of determining the fates of individuals that disappear.

Experimental and long-term descriptive studies of avian populations have shown that territorialism may limit breeding density on local areas (see Brown (1969); Klomp (1972); and Watson and Moss (1970) for reviews). A population surplus has been demonstrated by removal experiments in tetraonids such as red grouse, *Lagopus lagopus scoticus*, (Watson and Jenkins 1968), sharp-tailed grouse, *Pediocetes phasianellus*, (Rippin and Boag 1974), and rock ptarmigan, *Lagopus mutus*, (Watson 1965), as well as blue grouse.

Since survival of my radio-tagged yearlings was high and most birds established, there was little evidence for the existence of a surplus. The fates of 7 young which did not enter the population suggest that some may be subject to high predation pressure because of their wide movements, and, if they survive, may be delayed in reproduction beyond the time when recruitment is possible in that year.

A more substantial segment of my birds did not enter the population on prime habitat. These were young which entered sub-optimal habitats and bred, in the case of hens, or localized, in the case of males. Young which failed to enter the population on prime habitat may have survived and remained on the area if vacancies had been created by removing residents. Thus, these yearlings may be equivalent to replacement birds in removal experiments. I must emphasize that very densely forested areas were assumed to be sub-optimal habitat for blue grouse based on past studies on other areas (e.g. Bendell and Elliott 1966). Since these areas were not censused, this assumption is only tentative.

Exclusion of excess birds and mammals of several species from prime habitats, and their retreat to marginal areas, has been postulated by numerous authors (Kluyver and Tinbergen 1953; Tompa 1962; Carrick 1963; Errington 1941; 1963; and others). In tetraonids, examples of subordinate birds occupying poor habitats after ejection from preferred habitats are given by Jenkins et al. (1963) for red grouse and Moss (1972) for rock ptarmigan.

Radio-tagged young of both sexes varied markedly in their timing of recruitment and apparently in the quality of habitats they entered. Frequency and intensity of interaction between established birds and wandering young may be important factors determing whether they enter the population readily, are delayed, or fail to do so. Adult females occupied smaller pre-nesting home ranges, localized

earlier in their breeding cycle, and nested earlier than young hens. Thus, once a bird is established, it appears able to defend its area from newcomers. The major period of recruitment coincides with a reduction in the size of "defended" area of established hens as they begin to nest. This would lessen the frequency of interaction between established and unestablished birds, as suggested by Hannon (1978) for blue grouse and Herzog (1977) for spruce grouse (*Canachites canadensis franklini*), allowing wandering young to enter the population.

In both males and females, entry into sub-optimal habitat may be a response to their inability to locate unoccupied breeding sites on prime habitat. Although reproductive success of such birds may be lower (of 6 hens nesting, only 1 raised a brood), the reproductive rate of the entire population may be maximized (see Brown 1969; Krebs 1971).

Inherent differences among young may determine whether they establish in low-density breeding populations in marginal habitats or remain to "compete" for breeding sites on more crowded prime habitats (Chitty 1970). Also, if marked differences in such behavioural traits as "wildness" (Zwickel *et al.* 1977) occur between surplus birds and those more likely to enter the population, surplus young may be difficult to census. If surplus young are more difficult to approach, they may be under-sampled by our capture technique.

Hannon (1978) showed that once localized, yearling hens enter a rapid phase of gonadal recrudecence which leads to laying of the first egg in about 10 days. Since most radio-tagged young were recruited 12-15 days prior to laying their first eggs, they entered the rapid phase of recrudescence immediately after localizing. Thus, localization may trigger recrudescence and a delay or absence of breeding may be a result of being unable to localize on a breeding area because of interaction with established hens.

Cues asssociated with localization appear to trigger physiological changes that result in a higher level of aggressiveness. Hannon (1978) postulated that spacing of hens and the delay in recruitment of yearlings may occur by avoidance of areas occupied by aggressively vocalizing hens. Herzog and Boag (1977) found that yearling female spruce grouse would sometimes flee from playbacks of aggressive calls of hens and would not call aggressively until they themselves had localized for breeding. Bendell and Elliott (1967) reported that blue grouse hens were spaced evenly over breeding range in spring. Movement data from my study, as well as physiological and behavioural data obtained by Hannon (1978), support the conclusion of Herzog and Boag (1977) that aggressive behaviour associated with female territoriality appears to be a proximate mechanism for adjusting density of females.

Movement patterns of young males are more difficult to

interpret. Available data indicate that those that enter the population return to a part of their yearling home range as adults. If familiarity is a critical component of territorial establishment, a compromise must exist between having a home range as a yearling that is large enough to have a probability of replacing an adult male that dies; yet small enough that familiarity or dominance associated with familiarity can be attained. Whether young males are occupying exclusive areas or sharing portions of each others home ranges is not known for sure. However, in 2 cases where young males occupied immediately adjacent areas, there was little overlap of the activity centres of their home ranges (Sopuck 1978).

As in yearling hens, the ability for young males to enter the population varies markedly. The mechanism by which this occurs is difficult to determine because of their secretive nature. However, adult males have been observed to chase yearlings from their territories. My data, as well as those of Lance (1970), indicate that young males avoid territories of adults. Hooting, the territorial song of adults, may serve to space young males in areas between territories. Furthermore, young males may interact among themselves in these interstices, thereby limiting the numbers which settle.

In summary, only a few yearlings of both sexes failed to enter the population. Among successful yearlings, however, many were delayed in recruitment, likely as a

result of interaction with established birds. A gradient in patterns of movement by yearlings was evident and included those that localized soon after arrival on breeding range and those that tended to move widely well into the recruitment period. Young that fail to locate and maintain breeding sites on prime habitat may enter marginal areas to do so.

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S.J. Hannon provided data on the movements of nine radio-tagged hens which she followed during the 1977 breeding season on the same study area.

Work was conducted on lands of Crown Zellerbach of Canada Ltd., Courtenay Division.

Table 1. Numbers of radio-tagged grouse successful or unsuccessful in entering breeding populations, in relation to quality of habitat, 1976 and 1977. Percentages are in parentheses.

Fate	Yearlings Males N=29	Yearlings Females N=46	Yearlings Total N=75	Adults Females N=13
All habitats				
Successful	25(86)	43(93)	68(91)	13(100)
Not successful	4(14)	3(7)	7(9)	--
Prime habitat				
Successful	20(69)	37(81)	57(76)	13(100)
Not successful	3(10)	2(4)	5(7)	--
Total	23(79)	39(85)	62(83)	--
Sub-optimal habitat				
Successful	5(17)	6(13)	11(14)	--
Not successful	1(4)	1(2)	2(3)	--
Total	6(21)	7(15)	13(17)	--

Table 2. Numbers of radio-tagged grouse that were considered localized or wide-moving in spring, 1976 and 1977. Percentages in parentheses.

	Localized	Wide-moving
Yearling males N=30*	17(57)	13(43)
Yearling females N=46	18(39)	28(61)
Total N=76*	35(46)	39(54)
Adult females N=13	11(85)	2(15)

* includes 1 male that was located 8 km from his capture site, but is not included in Table 1 because only 1 location was made after his movement from the study area.

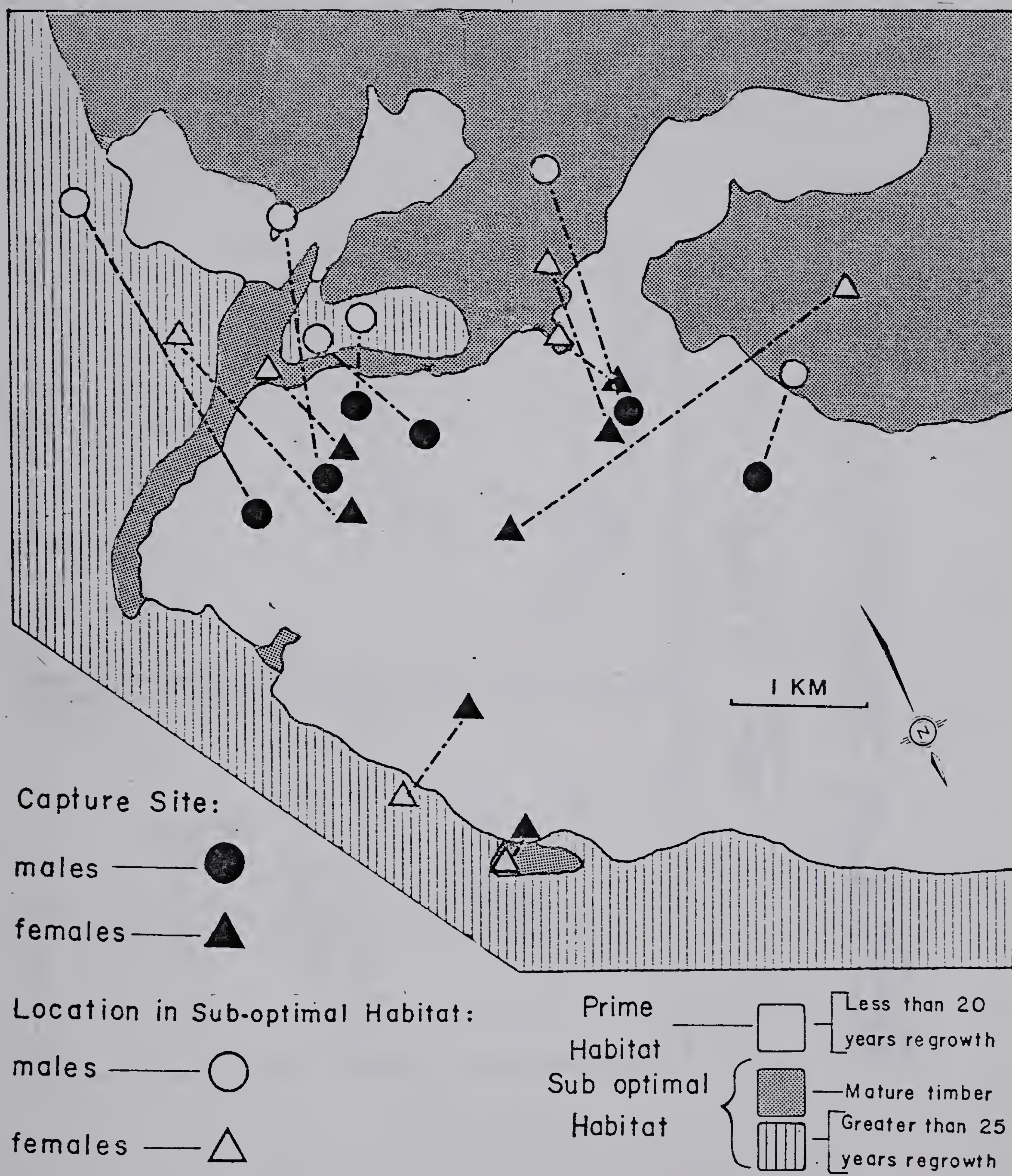

Figure 1. Entry into sub-optimal habitat and subsequent site attachment by yearlings radio-tagged on prime habitat, 1976 and 1977.

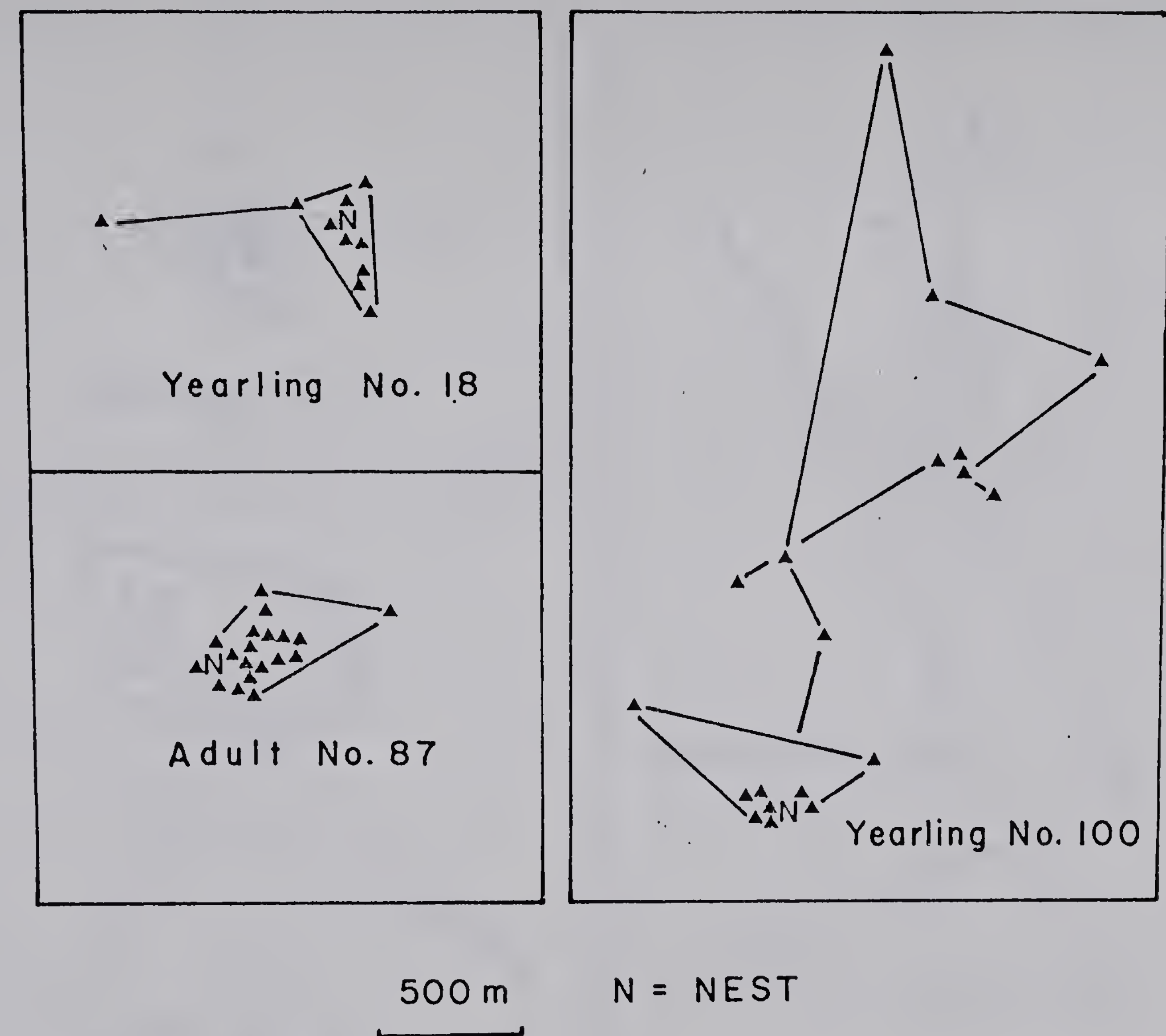

Figure 2. Examples of localized (No. 18 and No. 87) and wide-moving (No. 100) patterns of movement in yearling and adult hens.

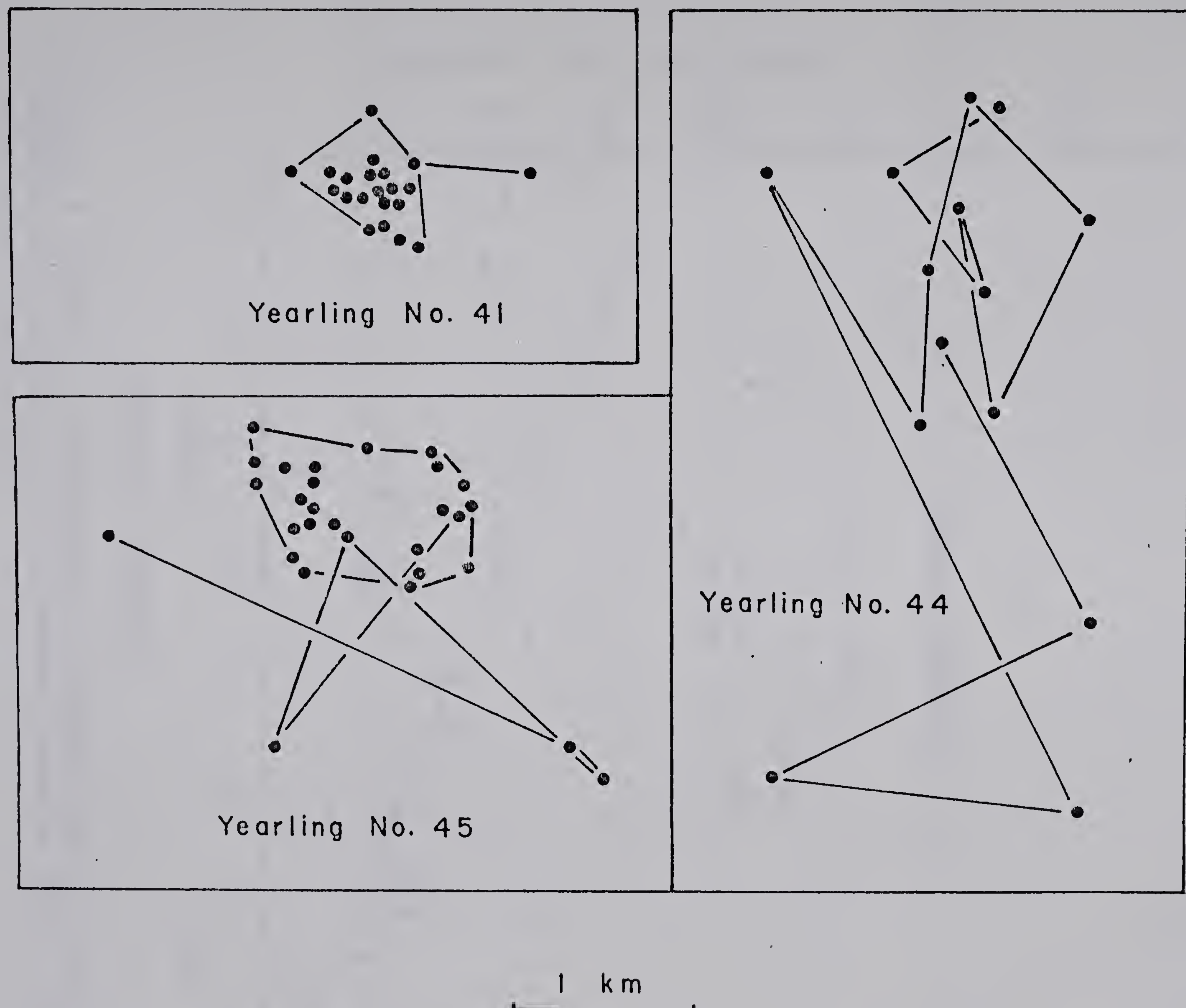

Figure 3. Examples of localized (No. 41) and wide-moving (No. 44 and No. 45) patterns of movement in yearling males. No. 44 did not localize, while No. 45 eventually did so.

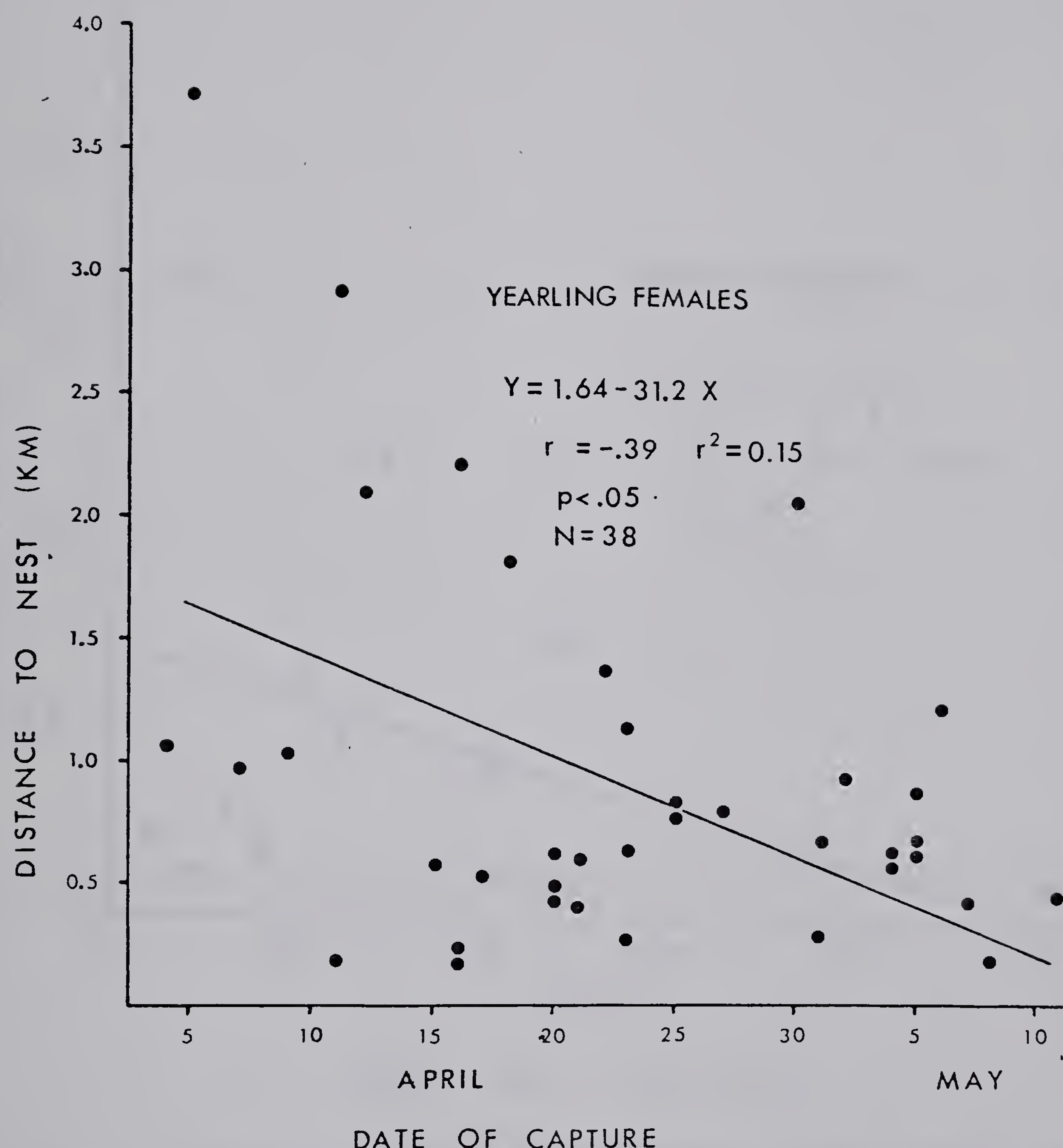

Figure 4. Relationship between date of capture and the straight-line distance from capture point to subsequent location of nest site for radio-tagged yearling hens.

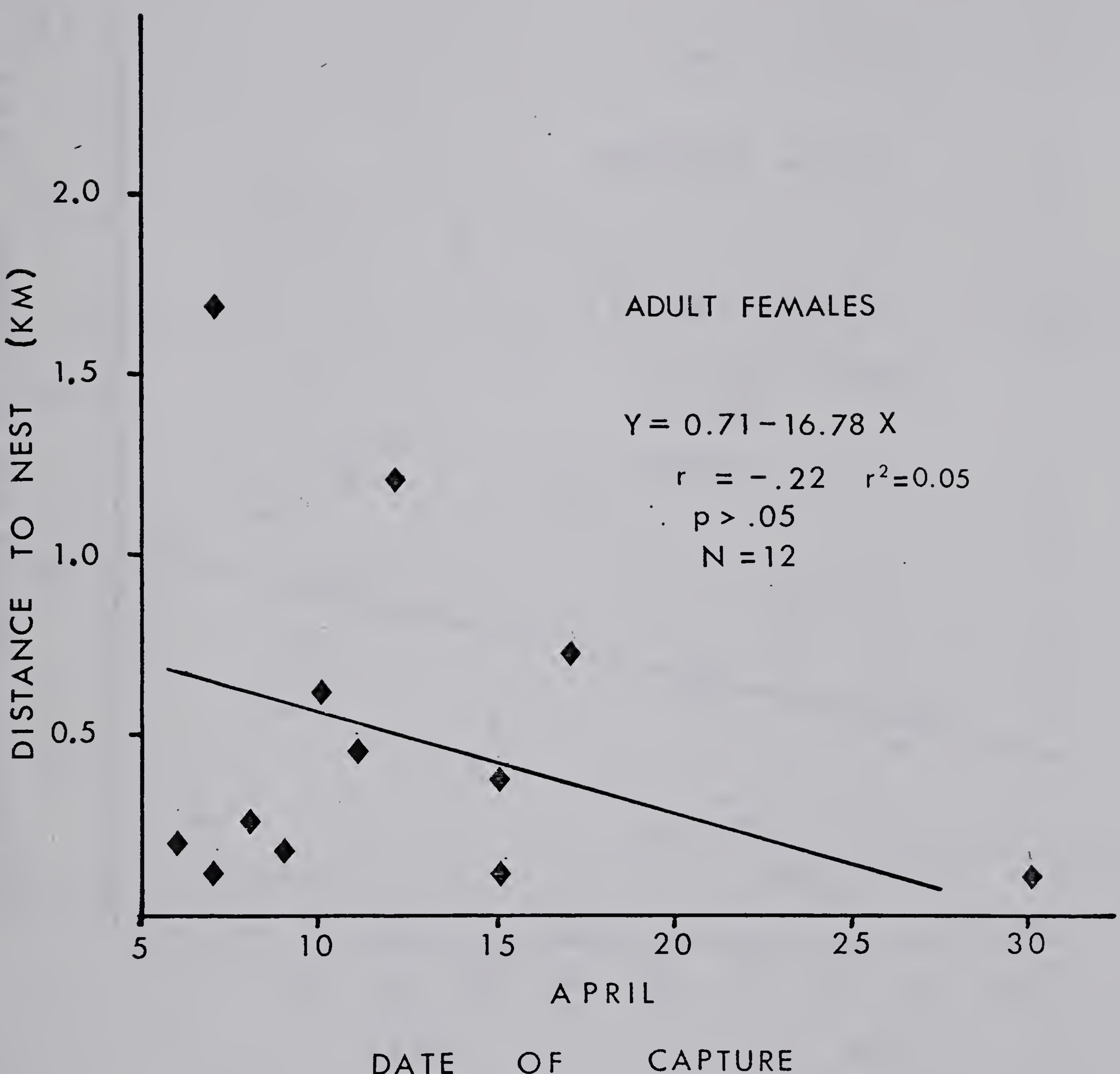

Figure 5. Relationship between date of capture and the straight-line distance from capture point to subsequent location of nest site for radio-tagged adult hens.

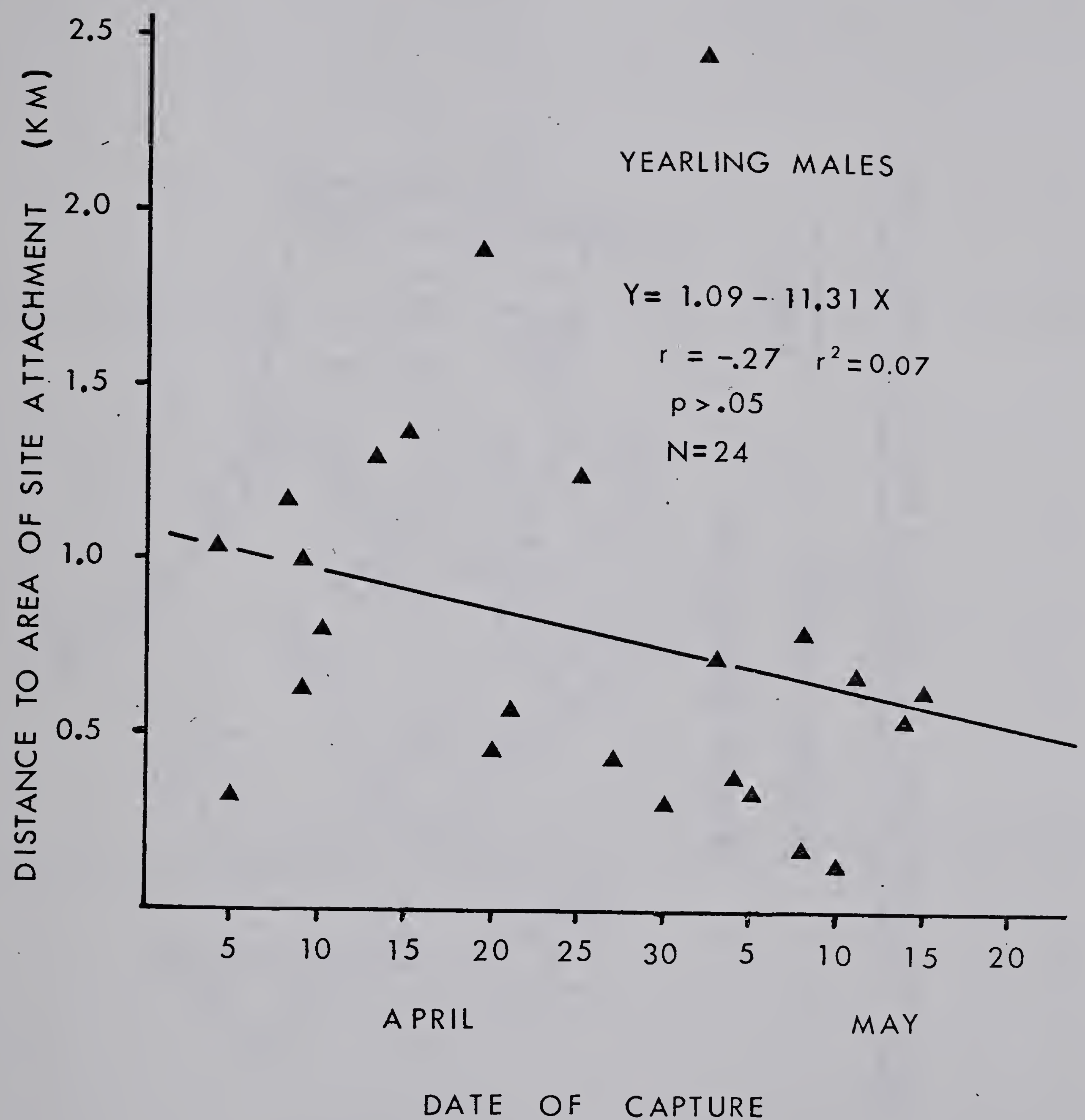

Figure 6. Relationship between date of capture and the straight-line distance from capture point to subsequent area of site attachment for radio-tagged yearling males.

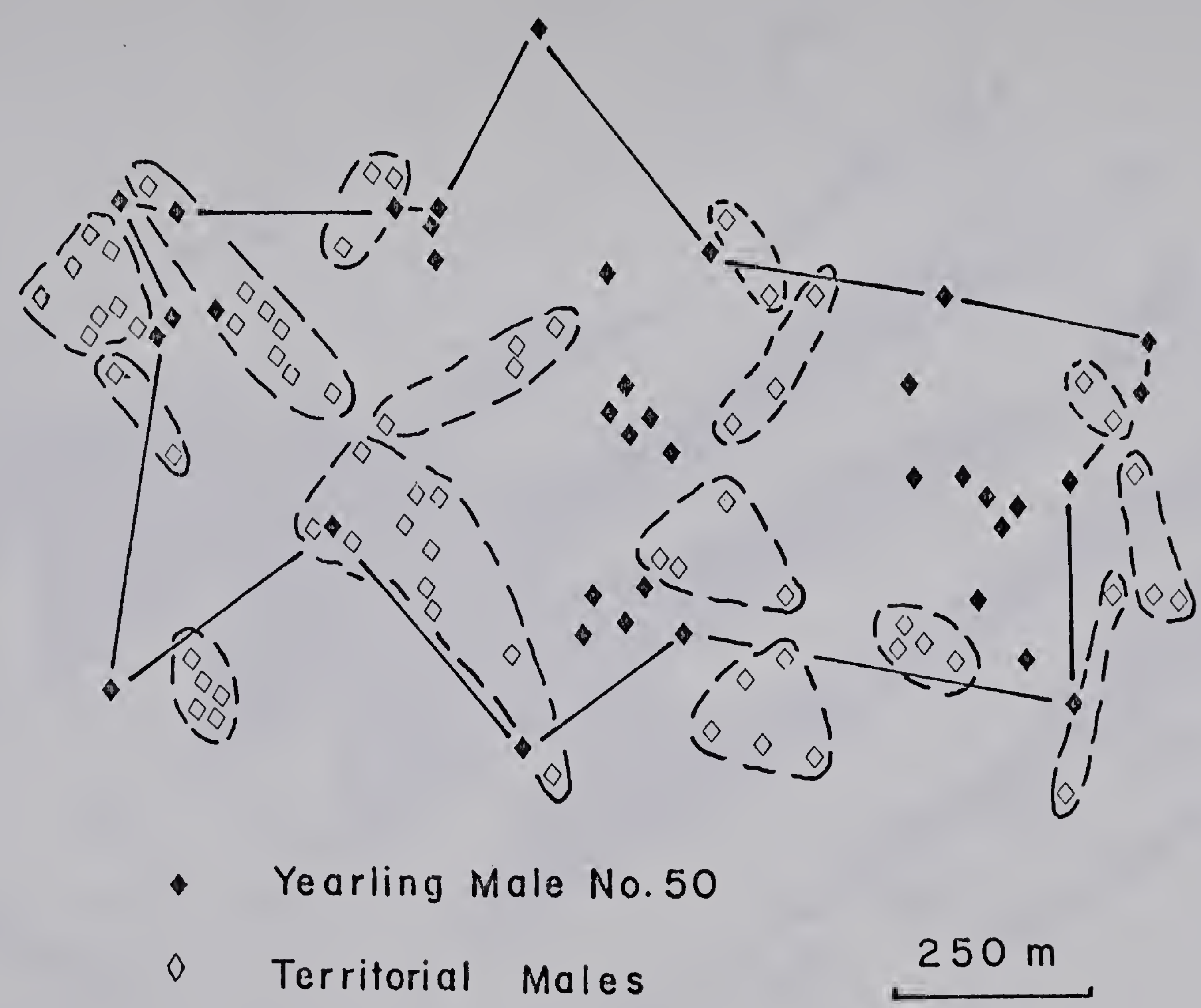

Figure 7. Comparison of a yearling male home range (No. 50) and the distribution of adult male territories on and near his home range.

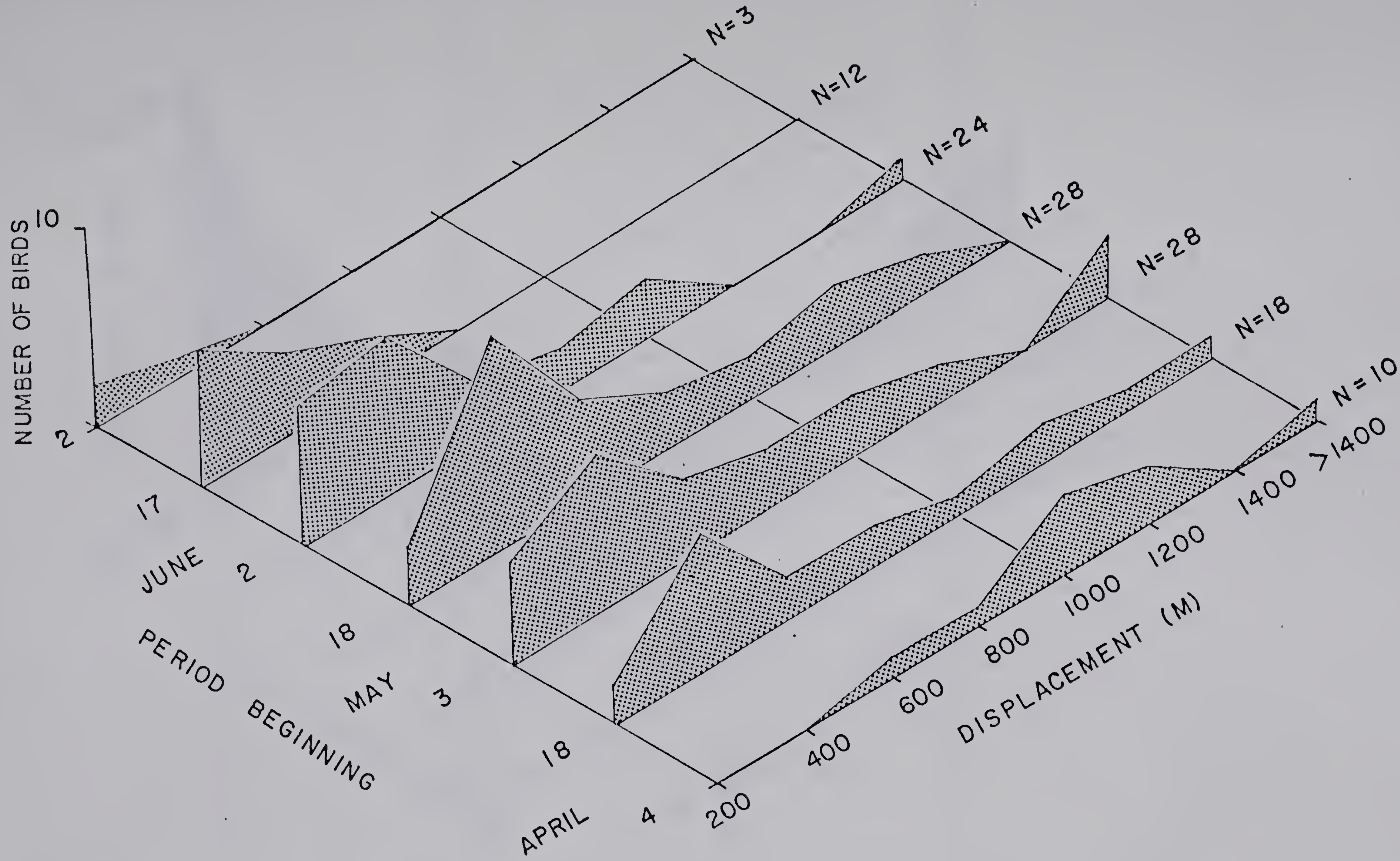

Figure 8 . Displacements of yearling males by 15-day intervals during the recruitment period.

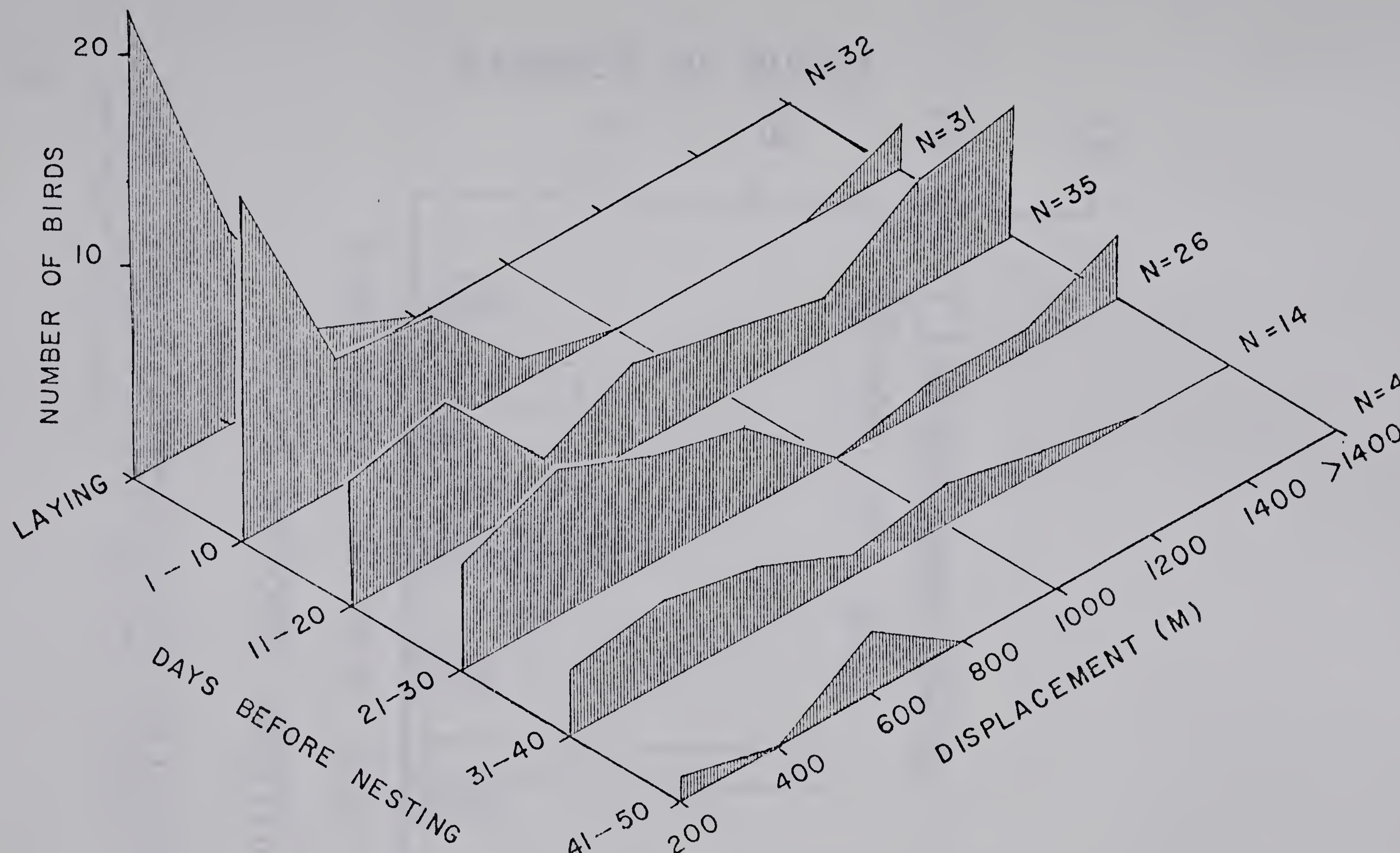

Figure 9. Displacements of yearling females by 10-day periods up to laying.

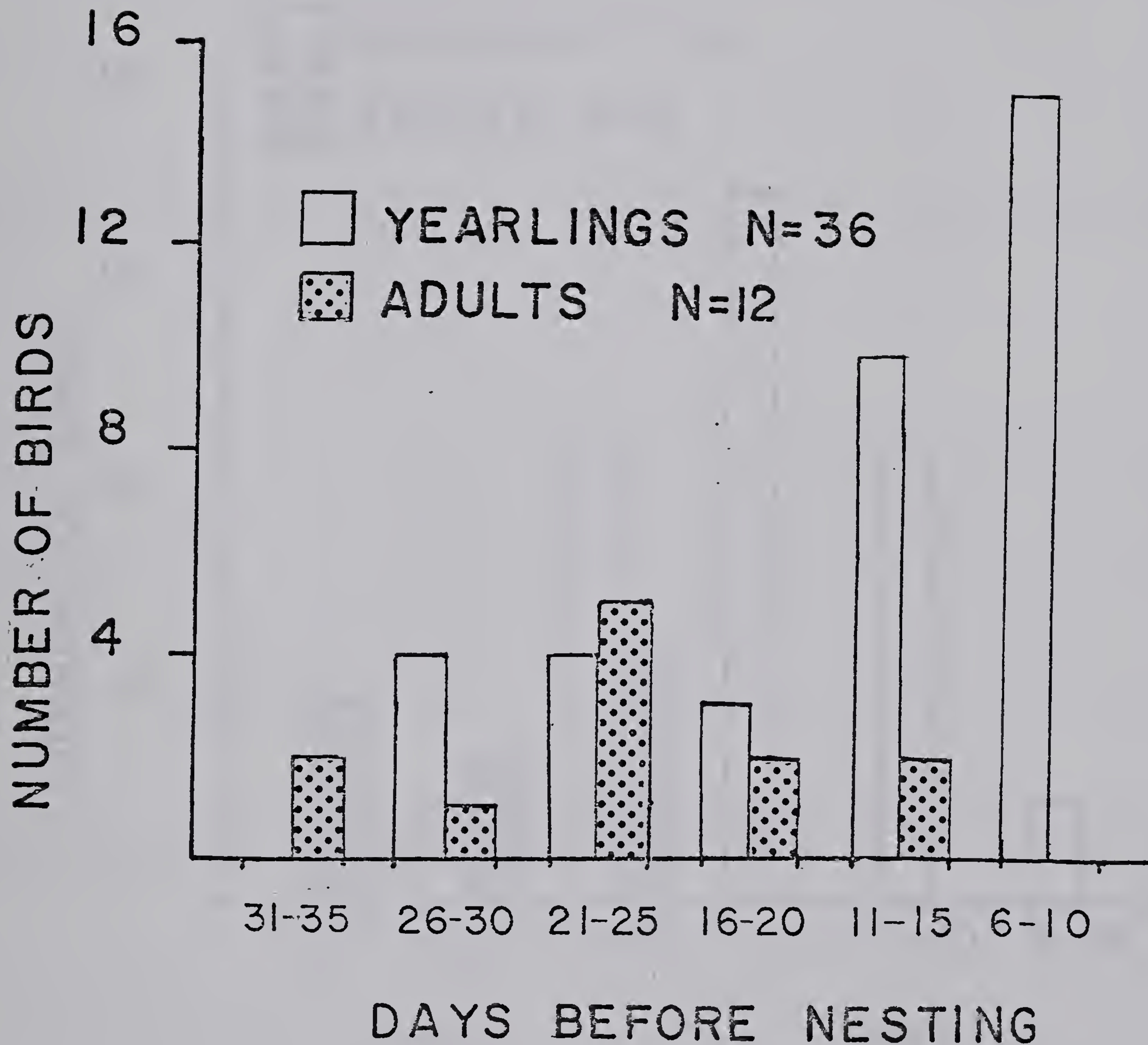

Figure 10. Timing of recruitment (yearlings) and localization for breeding (adults) in radio-tagged hens in relation to days before nesting (DBN).

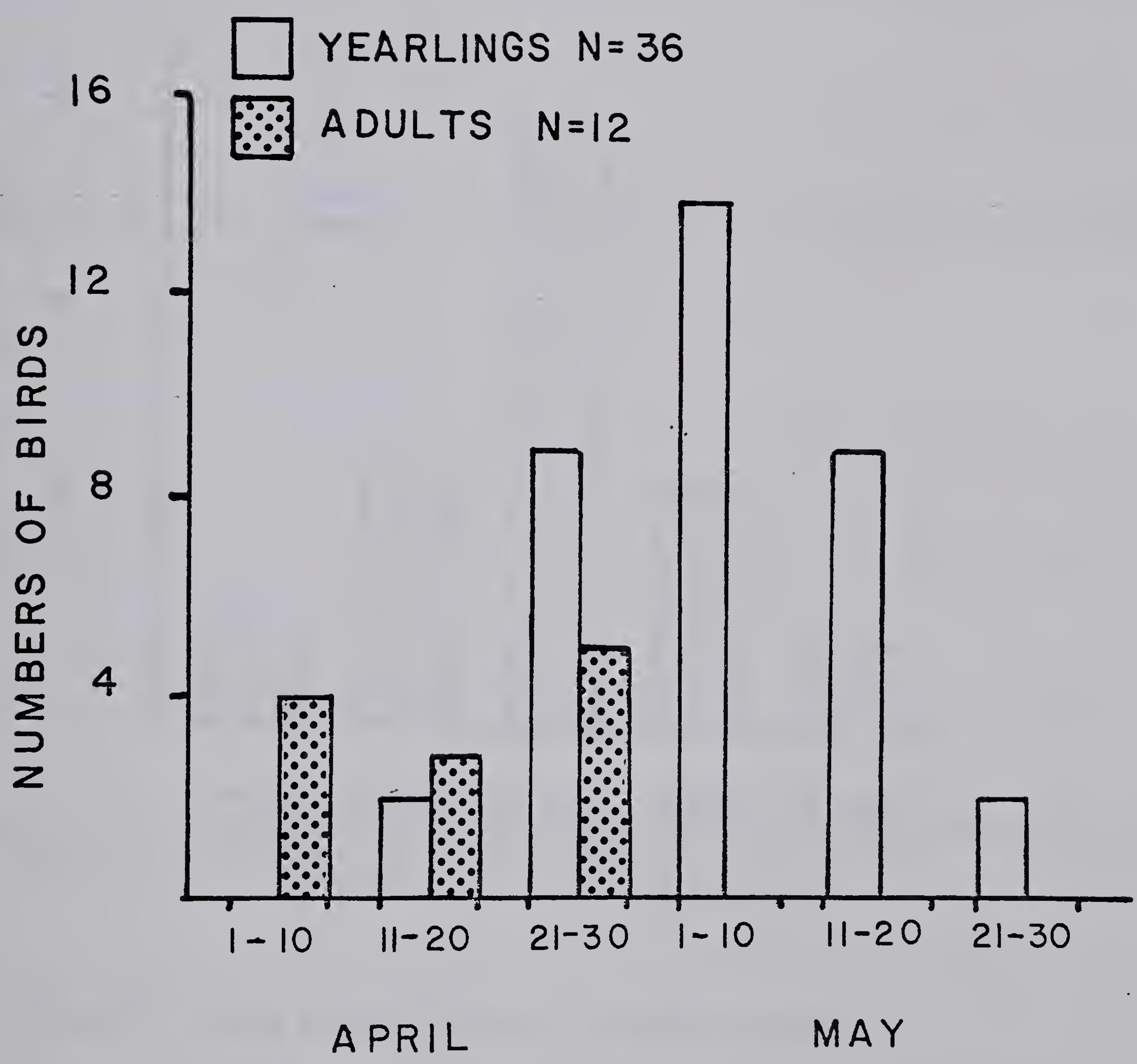

Figure 11. Timing of recruitment (yearlings) and localization for breeding (adults) in radio-tagged hens, using chronological time.

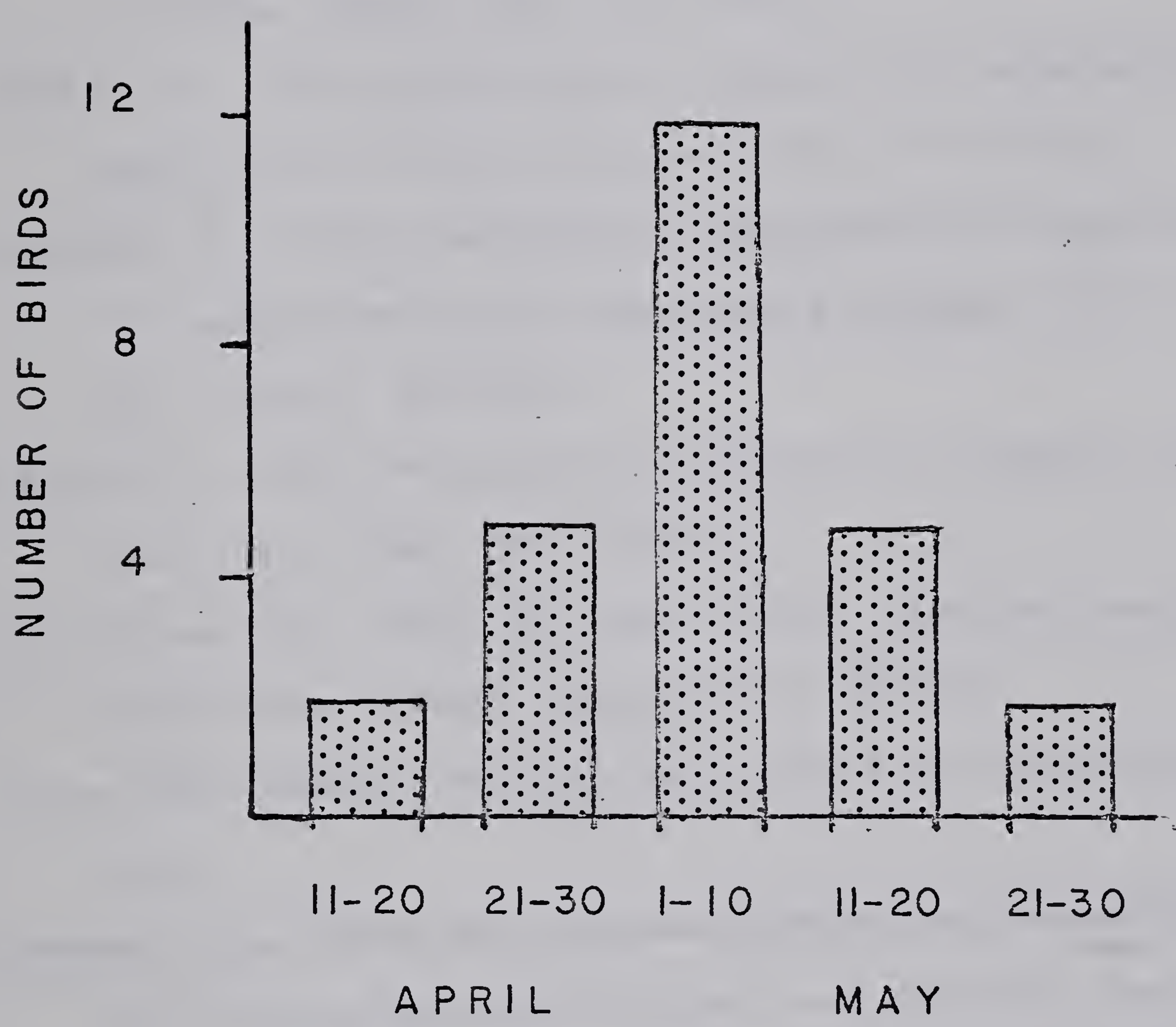

Figure 12. Timing of recruitment in yearling males.

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PAPER 2. Movements and Migration of Blue Grouse After the Nesting Period

Introduction

Movements of hens after they leave their nests, either with or without broods, have seldom been described for tetraonids. Broodless hens, especially, have received little attention because of their secretive nature (Bendell and Elliott 1967). Yearling males, presumed to be non-breeding in blue grouse, are also highly secretive and their movements during summer are poorly known (Zwickel and Bendell 1967).

A relatively large sample of blue grouse (*Dendragapus obscurus fuliginosus*) hens and yearling males was monitored by radio-telemetry during the springs and summers of 1976 and 1977. The objective was to document the movements of hens after they leave their nests and of hens and yearling males up to and including migration to winter range. The importance of these findings in relation to interpretation of data on population processes is discussed.

Study Area and Methods

Blue grouse were captured on a 1200 ha study area in the foothills of east-central Vancouver Island. The area was logged and/or burned less that 20 years ago and bordered by mature forest or dense second growth. Further details can be found in Zwickel (1977), Hannon (1978), and Sopuck (1978). Birds were outfitted with radio-transmitters in April and early May, 1976 and 1977, usually 2-4 weeks before they nested (in the case of females). Radio-locations of each bird were made about every 2 days on the summer range and, less frequently, by aircraft, in more remote areas. When possible, birds were approached on foot and sighted.

Home ranges were determined using the minimum polygon method as described by Harvey and Barbour (1965) and modified by Herzog (1977). Movements of hens are described beginning within 2 days after loss of nests, hatching of clutches, or loss of broods.

Except where specified, chi-square tests for independence or Student's t-tests were used in statistical analyses. Mean values are presented plus or minus one standard deviation.

Results

Movement data were obtained on 20 brood and 30 broodless hens starting immediately after leaving the nest and monitored for an average of 28 days. Movements of 22 yearling males were monitored during May through June. Information on adult males was obtained from past and concurrent studies in the same area. During migration, 10 hens without broods, 1 with brood, and 11 yearling males were located 1 or more times.

Movements of Hens With Broods

Movements of hens with broods up to 1 week after hatching were examined to determine possible effects of selection of nest sites and the age of the hens on early brood movements (Table 1). During this first week, daily movements were obtained. All adult hens (4) remained within 400 m of their nests, while 44% (7/16) of the yearlings moved at least 500 m away from the nest site. Two yearlings nested in densely forested areas and travelled to more open brood ranges over 1 km away. However, for most hens that made long distance movements no obvious change in habitat was evident. Seven hens accumulated a distance of more than 1 km between successive radio-locations (i.e. total straight-line distance travelled). Two were adults that remained in the vicinity of their nests. Thus, some broods travelled widely and far from their nests, while others remained near their nests, yet moved extensively. Although

samples are small, on average, yearlings travelled further from their nests than adults.

Cumulative brood ranges increased steadily throughout the period of study. On average, broods occupied areas of similar size during five 2-week periods after hatching (Figure 1). Movements of individual broods, however, indicate that 64% (7/11) travelled more widely during the first 2 weeks after hatch than during the following periods. For yearlings, at least, brood movements can be described as an initial period of wandering, then localization followed by expansion. Three broods monitored for over 6 weeks moved extensively, resulting in greatly expanded home ranges from 6 to 10 weeks after hatching.

Sizes of brood ranges of individual females were highly variable. For example, cumulative brood ranges ranged from 2 to 20 ha at 4 weeks, and 6 to 29 ha at 6 weeks after hatch, but this was due primarily to 2 hens that had extremely large movements.

No differences were apparent between average sizes of brood ranges of adult and yearling hens. However, 1 yearling occupied a very large area which, at 6 weeks after hatch, was 44% higher than any other hen (29 ha). By contrast, another yearling had a very small brood range; only 6 ha at 6 weeks after hatch.

Movements of Hens Without Broods

Cumulative home ranges of hens without broods increased

steadily (Figure 1). Migratory movements, that occurred prior to those of brood hens, are excluded from home range calculations. Eleven of 30 (37%) broodless hens made sudden directional movements ranging from 1 km to 3.2 km immediately after losing their clutches. Ten of these hens entered densely forested areas. Home ranges could not be calculated for 7 of these hens because they continued to move very widely. Thus, home ranges presented in Figure 1 include only broodless hens that localized soon after loss of nests or early broods, or moved widely followed by a period of localization.

On average, hens without broods occupied areas of similar size during four 2-week periods after loss of clutches or chicks (Figure 1). However, 58% (11/19) of the broodless hens monitored at least to 4 weeks after loss of clutches or chicks, occupied larger areas during the first 2 weeks after loss than during each of the following periods. Forty-three percent (12/28) had the centres of their home ranges at least 500 m from their nests. Some hens, therefore, moved directionally immediately after losing their nests and then gradually expanded their ranges at a suitable area some distance from their nests. Others remained near their nests and expanded their ranges from that point.

As with brood hens, there was considerable variation in the sizes of home ranges of individual females. At 4 weeks after loss of clutches or chicks, broodless ranges varied

from 3 to 26 ha and from 5 to 31 ha at 6 weeks after loss. Only 2 adults were monitored without broods, and both occupied the smallest areas of 9 females that were monitored for at least 6 weeks.

Habitat Use of Hens With and Without Broods

Ten brood and 10 broodless hens were chosen at random and their locations throughout summer were examined to see if the two groups differed in selection of vegetative cover. Eighty percent (127/158) of the locations of broodless females were in, or on the edge of, thickets; only 24% (33/139) of brood hen locations were in this type. Clearly, broodless hens were found more often in thickets than brood hens ($p<.001$). Brood hens selected more open areas and were often seen well above ground level, perched on logs or stumps. Broodless hens held tightly in thickets when approached and were difficult to see. This secretive behaviour contrasted sharply with the obvious distraction display of brood hens when approached by an observer.

Departure From Breeding Range

The directions, distances, and elevations attained during the initial stages of migration to winter range by 10 broodless hens, 1 brood hen, and 11 yearling males are shown in Figure 3. In most cases, permanent wintering areas were likely not reached.

Migration of hens without broods

On average, broodless hens remained on breeding range until at least 11 July (n=28), 28 days after loss of nests or young broods. Since some transmitters were removed about this time, the exact dates of departure for these hens were not determined. However, migration of 10 broodless females from breeding range was monitored. Time of departure varied markedly, the average date being 19 July (range: 14 June to 22 August). On average, hens followed during migration remained on breeding range about 4 weeks after nest or brood loss (range; 3 to 57 days).

Migration was initiated by a sudden, directional movement to the west or southwest (241°±29, on average), usually the most direct route to upland coniferous forests. The mean straight-line distance travelled was 6.4 km (range: 1 to 20). The mean elevation attained by migrating broodless hens was 1340 m, (range: 700 to 1980). Two hens which had migrated 7 and 15 km were located 2 weeks later in the same areas. These birds may have completed migration, but most data presented here are likely for hens en route to winter range.

Only for 4 hens could reasonable estimates of rates of travel be made. The rates of travel and distances attained are as follows: 1.2 km/day (20 km in 17 days), 1.8 km/day (14 km in 8 days), 1.8 km/day (7 km in 4 days) and 1.0 km/day (4 km in 4 days).

Migration of broods

Bendell and Elliott (1967) reported that at least half of the hens with broods on their lowland study areas on Vancouver Island had begun to migrate between 1 September and 15 September. They felt that few brood hens left before the end of August. Lance (1970) followed a brood that left breeding range on 1 September. In my study, only 1 brood was monitored during migration. This brood began to migrate on 3 September, with a sudden long movement into upland forests to the southwest. Nine days later the hen and 3 chicks were in sub-alpine parklands at an elevation of 1700 m and 15 km from their lowland brood range. They travelled about 1.7 km per day, on average. Three radio-tagged broods were on breeding range at least until 1 September. Two others had their transmitters removed on 22 August and were still on their summer home ranges. These data suggest that most broods do not migrate until the end of August, 2 to 6 weeks later than broodless hens, thus agreeing with the suggestion of Bendell and Elliott.

Migration of yearling males

Yearling males remained on breeding range, on average, until at least 21 June (n=22, range: 3 June to 13 July), about 60 days after arrival [banding records suggest that yearling males arrive on breeding range in

mid-April (F.C. Zwickel - unpubl. data)]. The mean date of departure of 11 yearling males that were monitored during migration was 18 June (range: 3 June to 27 June); about 8 weeks after their arrival. Again, initiation of migration was by a sudden movement to the west or southwest (245°±30 on average), the most direct route to upland forests. The average straight-line distance travelled was 6.3 km (range: 1 to 9 km) and an average elevation of 1350 m was attained. Two males were located twice in the uplands (3 weeks between locations) on adjacent sub-alpine ridges. These males may have reached winter range after having travelled 6 km from their summer ranges and attaining an elevation of 1400 m.

Behaviour of Adult and Yearling Males in Summer

Of 50 individually marked adult males observed singing on their territories in May of 1976, 28 (56%) were observed singing at least once after 15 June. Singing by males that were identified individually dropped off sharply in July, but 1 was still seen singing on 6 August. This suggests that many adult males are still on territories at the time when most yearling males have initiated migration.

While on summer range, yearlings were highly secretive as they were never seen in courtship display and often utilized thickets or areas of dense vegetation. Yearling males were compared with radio-tagged broodless hens as to use of thickets. Of 215 sightings of yearling males 72% were

in thickets which did not differ significantly from broodless hens ($p>.05$). Yearling males often held tightly under cover and were difficult to see. By contrast, adult males are often seen courting brood or lone hens and may sing on territories after mid-June.

Discussion

Sizes of home ranges of female blue grouse with and without broods have not been reported. Bendell and Elliott (1967) obtained maximum distances between sightings of 48 brood hens from June to August. They found that 81% moved less than 1 km, compared to 57% (8/14) in my study. The smaller ranges reported by Bendell and Elliott may be because they restricted observations primarily to within the boundaries of their study area. Herzog (1977), working with spruce grouse (Canachites canadensis franklini), reported brood ranges averaging 29 ha (n=8) in size and ranges of broodless hens averaging 15 ha (n=11). Maxson (1978), working with ruffed grouse (Bonasa umbellus), found brood ranges averaging 15 ha (n=5) and broodless ranges of 8 ha (n=5). In my study, brood ranges averaged 14 ha (n=8, 6 weeks post-hatching) and broodless ranges 15 ha (n=9, 6 weeks after loss of nests or young broods). Thus, blue grouse have brood ranges similar in size to those of ruffed grouse, but apparently smaller than spruce grouse. This may be due to lower breeding densities of spruce grouse as compared to blue and ruffed grouse.

Broodless female blue grouse appear to travel more extensively than ruffed grouse and possibly spruce grouse. Although spruce and blue grouse had similar sizes of home ranges, only the localized portions of home ranges of broodless blue grouse were determined as I excluded wide movements of some hens immediately after nest break-up. The

relatively wide movements of blue grouse may be because the species is migratory. Although migration in broodless hens was initiated by an obvious movement to the southwest, pre-migratory restlessness may have caused earlier movement.

Many brood hens move extensively soon after their chicks have hatched and some may move long distances from their nests. This may relate to the dietary requirements of chicks. Godfrey (1975) thought wide movements by young ruffed grouse broods and a later restriction of movements, as occurred in my study, was because of a shift from insects to plants as the major item of food. Beer (1943) suggested that young blue grouse used open areas because of more abundant insects and other invertebrates. I found that 2 broods left their nests in densely wooded areas to enter more open brood range a few days after hatching.

Long distance movements from the nest by brood hens suggest that preferred brood range is not always associated with nest sites and may not be an important factor in the selection of nest sites. Many yearlings were delayed in nesting, likely as a result of aggressive interactions among birds (Sopuck 1978). Thus, new recruits may be selecting nest sites in areas not occupied by established hens, rather than for brood range in the immediate vicinity of the nest. If true, some hens might be expected to range widely after hatching. Limitation of recruitment may result from interaction among hens, therefore, rather than a lack of nesting sites in areas suitable for rearing broods; a

commonly suggested reason for territoriality and selection of nest sites (e.g. Lack 1966). However, Lance (1978) provided limited evidence that the nutritional quality of vegetation on breeding territories of red grouse available to the laying hen correlated with survival and growth of the brood. Nevertheless, the seven radio-marked brood hens followed by Lance moved long distances (unspecified) from the nest site and the pre-nesting feeding areas of the hen, while the chicks were a few days old. However, both my results and those of Lance suffer from the possibility that harassment associated with radio-tracking may have influenced the extent of movement away from the nest.

Since some broods travelled widely throughout summer, it is not known whether broods are spacing themselves. Some hens did not remain on their pre-nesting home ranges. Either these hens roam freely with their broods or they are forced to do so in response to interactions with other hens. Herzog (1977) found that spruce grouse broods were spacing themselves temporally rather than spatially. This may reduce predation on chicks and ensure optimal foraging by juveniles.

The observed behaviour and movements of broodless hens and yearling males, both unsuccessful at breeding, may be an evolutionary strategy to maximize survival until the next breeding season. In comparison to brood hens and adult males, their behaviour is more secretive, they select more dense cover, and they migrate earlier. Brood hens and

territorial males maximize their reproductive effort during the current breeding season, but this may lower their survival relative to broodless hens and yearling males. Adult males are still courting hens in June and early July and are hence more conspicuous than yearlings. Brood hens select open areas and distract predators from their chicks. Thus, brood hens and adult males may have higher predation rates than broodless hens and yearling males.

Information for birds on winter range is limited because birds were not located throughout winter. Initial stages of migration indicate that birds dispersed over a wide area. This is in agreement with Zwickel et al. (1968) and Bendell and Elliott (1967), who found that members of a population may be wintering far apart. However, little is known of the extent of interaction on winter range, especially between established members of a population and juveniles that may eventually follow them to a particular breeding range. This topic needs further study.

King (1968) could not locate wintering hens or juveniles. My findings indicate that some broodless hens and broods may be travelling longer distances than searched by King. As well, 2 juveniles located in late winter were located in more dense forests and at lower elevations than the open sub-alpine ridges searched by King.

In summary, considerable variation was evident in the movements of brood and broodless hens, with some restricting their movements, usually near their nests, while others

moved extensively, sometimes far from their nest sites. Yearlings may travel more widely than adults, both with brood and without. Timing of migration was also highly variable, but generally yearling males left breeding range first, followed by broodless hens and adult males, with hens with broods leaving latest.

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Table 1. Distances travelled by adult and yearling hens with broods 1 week after hatching their clutches.

Movement class (m)	Displacement from nest*		Total distance travelled**	
	Adults	Yearlings	Adults	Yearlings
0-500	4	9	1	5
500-1000	--	5	1	6
1000-1500	--	2	2	5
X±SD	205±81	484±333	949±529	737±421

* refers to straight-line distance from nest site to brood location at end of 1 week period.

** refers to the accumulated distance travelled between daily radic-locations of each brood during the 1 week period.

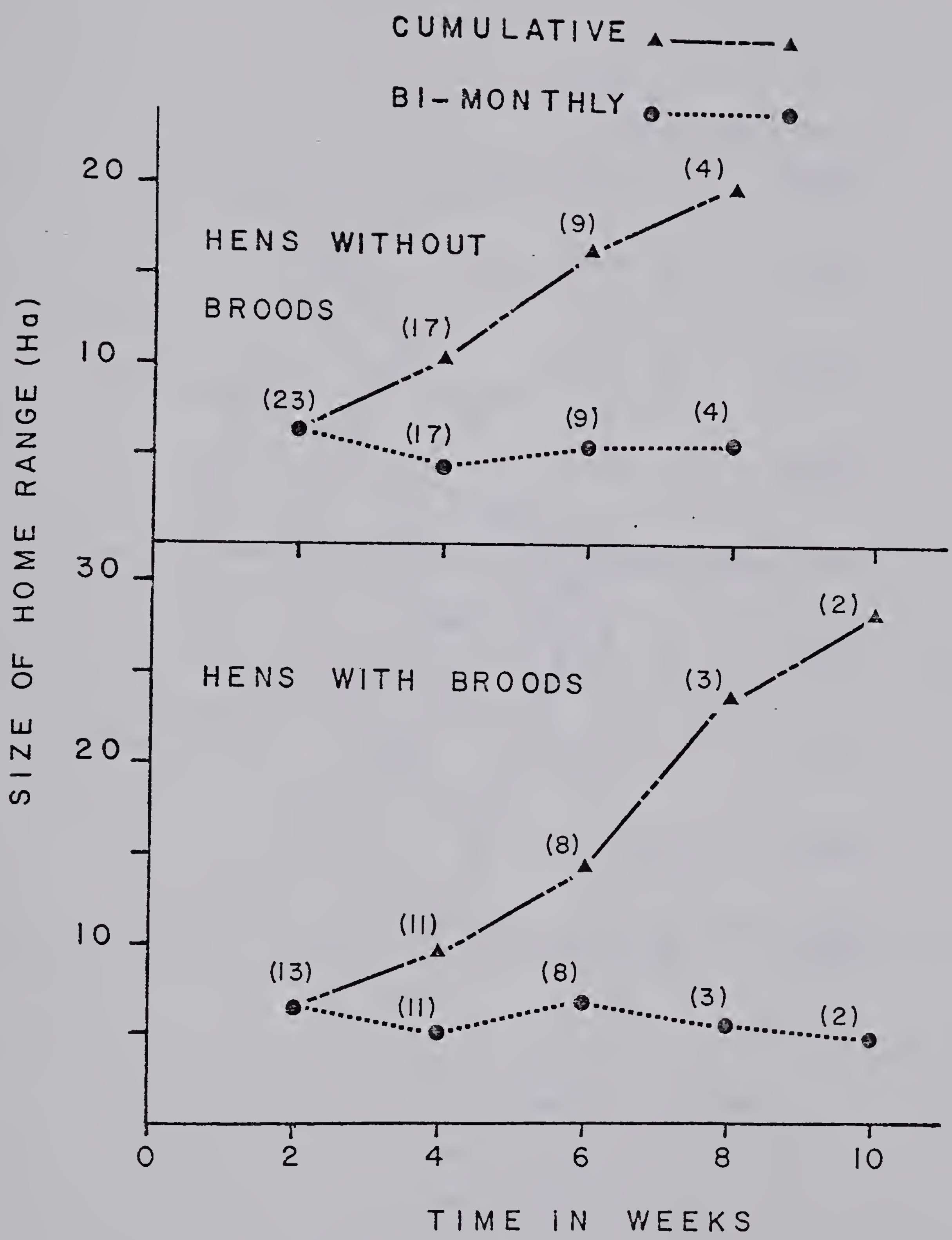

Figure 1. Mean sizes of cumulative and bi-monthly home ranges of brood and broodless hens. Sample sizes are in parentheses.

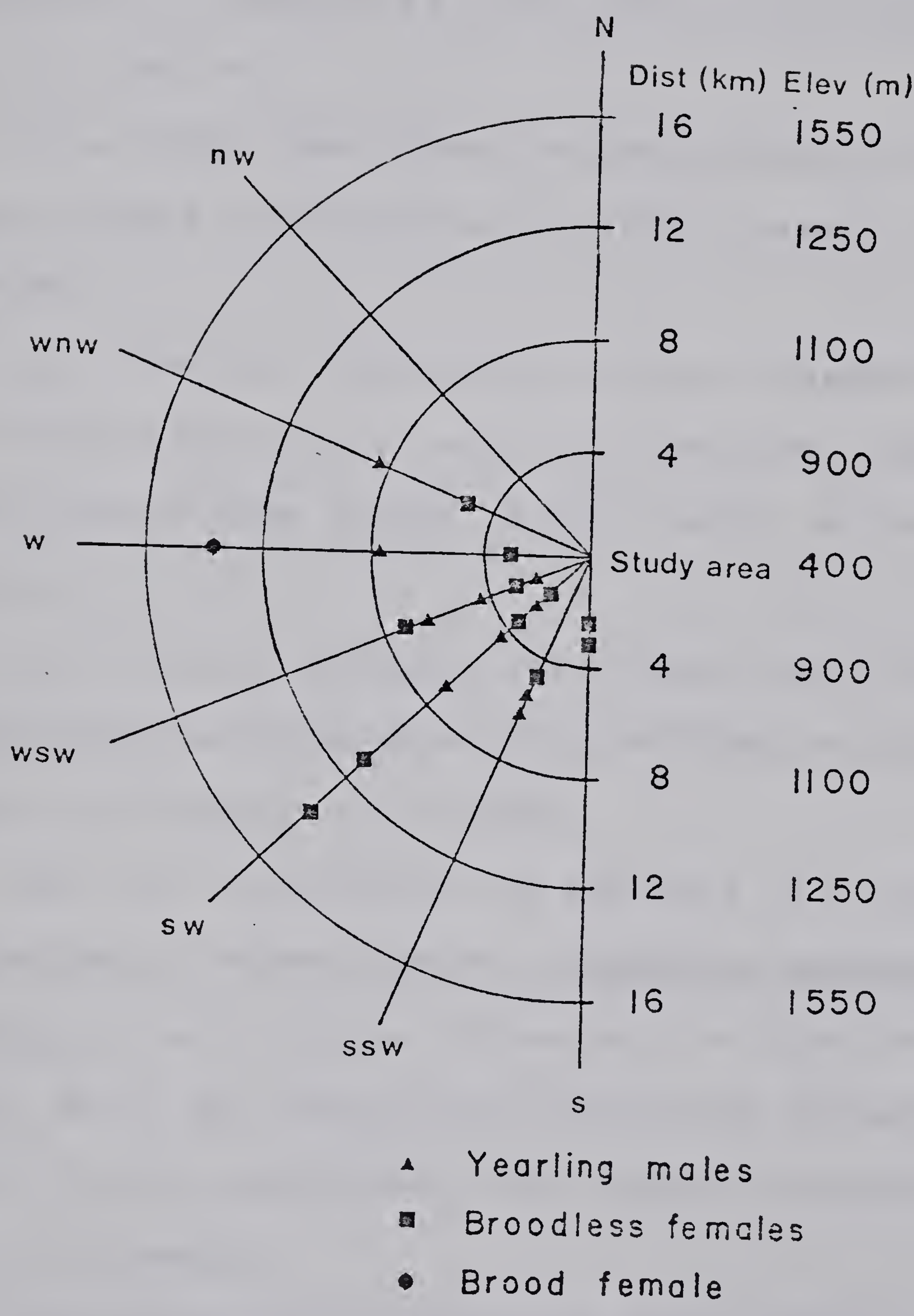

Figure 2. Length and direction of migratory movements of blue grouse from breeding range towards wintering areas, 1976 and 1977. Directions are to the nearest 22.5 degree compass line.

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CONCLUDING DISCUSSION

Populations of blue grouse are likely self-regulated, at least in prime habitats where extrinsic factors are not directly limiting numbers. Breeding populations are stabilized around a mean density by the exclusion of "surplus" potential recruits by established birds (Bendell et al. 1972 Zwickel 1972). Population regulation can be examined at two levels. There are ultimate factors that set the level at which a particular population is stabilized and a proximate mechanism adjusting breeding numbers to this level.

The ultimate factors are most difficult to study. Zwickel and Bendell (1972) found no correlation between several environmental parameters and densities of three populations of blue grouse on Vancouver Island. Watson and Moss (1972) postulated that the nutritional value of the vegetation on an area directly affects the physiology or aggressive behaviour of red grouse (Lagopus lagopus scoticus) resulting in varying capacities to adjust numbers. Another more general theory proposed by Chitty (1967) implies that environmental factors act indirectly by selection of genotypes affecting traits important to the process of adjusting breeding densities. Thus, the quality of individuals, mediated by behaviour, may determine how numbers are adjusted in a particular population.

Aggressive behaviour is most often cited as an important variable involved in the determination of

densities among populations. For blue grouse, Mossop (1971) and Bergerud and Hemus (1975) found that behaviour of territorial males from populations with widely differing densities was different. Robel (1972) thought that levels of aggression in male and female prairie chickens (Tympanuchus cupido) might be important in population regulation.

Movements of potential recruits examined in my study may reflect competition for breeding space; and hence would be a consequence of the proximate mechanism of regulation. Aggressive interaction between sub-ordinate and dominant individuals of both sexes in tetraonids has been observed (Robel and Ballard 1974; Watson and Moss 1971; Kruijt and Hogan 1967), but rarely have the fates of those excluded been determined. Based on the stability of populations of blue grouse on prime habitat, excluded birds have been assumed to be non-breeders that suffer high mortality (e.g. Bendell et al. 1972). My findings suggest that a substantial number of excluded birds do not die or fail to breed. Populations in sub-optimal habitats rarely have been censused and breeding numbers here may fluctuate with the size of the excluded "surplus" from prime habitats. To elucidate this problem, marginal habitats should be censused to better understand the relationship between populations here and those in prime habitats.

My findings suggest that yearlings may differ in their response to competition on prime habitat in spring. Different possible "strategies" available to potential

recruits are outlined in Figure 1. Most yearlings select open areas (i.e. prime habitat) when they arrive on breeding range (Bendell and Elliott 1967). Their fates may depend on different strategies to maximize their breeding potential. Assuming that birds on prime areas have higher reproductive success than those on sub-optimal areas, as suggested by limited data, most potential recruits may commit themselves to prime areas. In females, some of these birds may be delayed beyond the time when nesting is possible in that year and become non-breeders (Hannon 1978). Others may breed, but will be delayed. In males, the commitment is not as crucial as females because they are likely non-breeding in their first summer anyway; but their options are similar. Site attachment as yearling males may be critical in establishing territories as adults.

Some potential recruits may opt for sub-optimal areas. Chitty (1970) proposed that some genotypes will be at a disadvantage in dense populations and may do best in habitats that are least crowded. Lower breeding success in these areas may be compensated for by a lower frequency of interactions with established birds. Hence, females will be more likely to nest and males to show prolonged site attachment. Although my findings are limited to recruitment by yearlings, birds that enter marginal populations may attempt to breed in prime areas during subsequent seasons. Thus, populations in marginal areas may buffer or stabilize breeding populations in prime habitats when recruitment

potential is low.

An important question not addressed directly by my approach is: can "surplus" birds be distinguished from birds more likely to recruit? Zwickel et al. (1977) found no differences in several behavioural and morphological features between recruits recolonizing a removal area and recruits to an undisturbed control population. However, Redfield (1974) found that potentially surplus yearlings differed with respect to genotypes at one locus from yearlings that entered established populations. Also, Hannon (1978) reported that non-breeding females may weigh less than breeders.

The wide range of movement patterns exhibited by successful recruits in my study may be a result of intraspecific competition for breeding space. Yearlings that tended to be wide-moving may possess inherent traits which decrease their competitive abilities. In years of high recruitment potential, intensified competition may result in those yearlings being non-breeders or, if they survive in marginal habitats until their second year, they may be able to enter populations on prime habitat as 2 year olds.

As previously mentioned, only 9-13% of the sample of radio-tagged yearlings failed to enter the population and, excluding 4 birds that were killed by predators, only 4-8% can be considered a non-breeding surplus. However, the size of the surplus in a discussion of the mechanisms regulating a popualtion may be irrelevant, since it is crucial only to

demonstrate whether or not a surplus exists. The size of the surplus may fluctuate over time and regionally as well, due to the very nature of the regulatory process.

For example, there is some evidence that recruitment potential (i.e. number of juveniles surviving to their first spring) was lower than average during this study. During 9 years of study (1969-1977) on Comox Burn the 1975 and 1976 breeding seasons ranked only fifth and seventh in the number of chicks produced, respectively (based on late summer brood counts-F.C. Zwickel, unpubl. data). This productivity was reflected in the low numbers of yearlings censused on Comox Burn in the following springs of 1976 and 1977. The numbers of yearlings identified in 1976 and 1977 ranked only sixth and ninth, respectively, during the 9 years of study. Also, during the yearling-only removal on the experimental area, Tsolum Main (F.C. Zwickel, unpubl. data), only about one half as many yearlings were identified in 1976 as in 1975. In the post-removal year, 1977, the lowest numbers of yearlings were recorded during the entire 9 year period. Thus, if 1976 and 1977 were years of low recruitment potential, the probability of obtaining surplus yearlings in the radio-tagged sample may have been low as well.

A possible bias in my study is that "surplus" potential recruits may not be as readily captured by our techniques as those that are more likely to enter the population. Dispersing individuals in other animals are difficult to census. Hilborn and Krebs (1976) found that the fates of

disappearing *Microtus* could not be determined using only 1 trapping or monitoring technique. Further research is needed to alleviate this problem. Longer lived solar-powered radio transmitters may allow juvenile blue grouse to be radio-tagged in late summer when all individuals likely have similar probabilities of capture. Barring excessive mortality, this would provide an unbiased sample of potential recruits in spring.

The small number of "surplus" birds found in this study may simply be an artifact of the techniques used. A non-breeding surplus may not exist, at least in yearling females. For example, the 6 yearling hens whose nests were not found or were not checked for a brood patch, may have been inhibited from nesting by handling during capture and the presence of the radio-package. The driving force to nest appears to be very strong in yearling hens as shown by the high frequency of nesting in the radio-tagged sample. If this study demonstrates that a surplus (of any size) does not exist, it contradicts previous removal studies by Zwickel (1972) on a nearby area and Bendell *et al.* (1972) on an area 30 km away. Both studies showed that many more yearlings were present on the experimental area the breeding season following the removal than would have been necessary to maintain population stability if the removal had not taken place. However, neither study demonstrated that these "surplus" yearlings would have been non-breeders if they were not attracted to the area by the vacancies in

prime breeding habitat created by removals. The results of my study suggested that such birds may breed elsewhere such as in marginal habitats where competition for breeding space may be less intense.

I also investigated, as a secondary objective, aspects of nesting and post-nesting biology of females and summer and migratory movements of yearling males. The potential differences in the contributions of yearlings and adults to production may be important in explaining yearly variations in productivity. Although Zwickel and Bendell (1967) have shown that size of the breeding population is independent of variations in productivity, they were dealing with areas of prime habitat. As they did not census breeding numbers in marginal habitat, population fluctuations in these areas may be correlated with variations in productivity.

Marked variation in the movements of hens with and without broods, and in the timing of migration of broodless hens and yearling males may reflect general inherent differences among yearlings that relate to their ability to recruit. For example, some yearlings with and without broods moved extensively, relative to adults. Early migration of unsuccessful breeders may increase their probability of breeding in subsequent years. Further work is necessary to examine differences among yearlings in relation to recruitment.

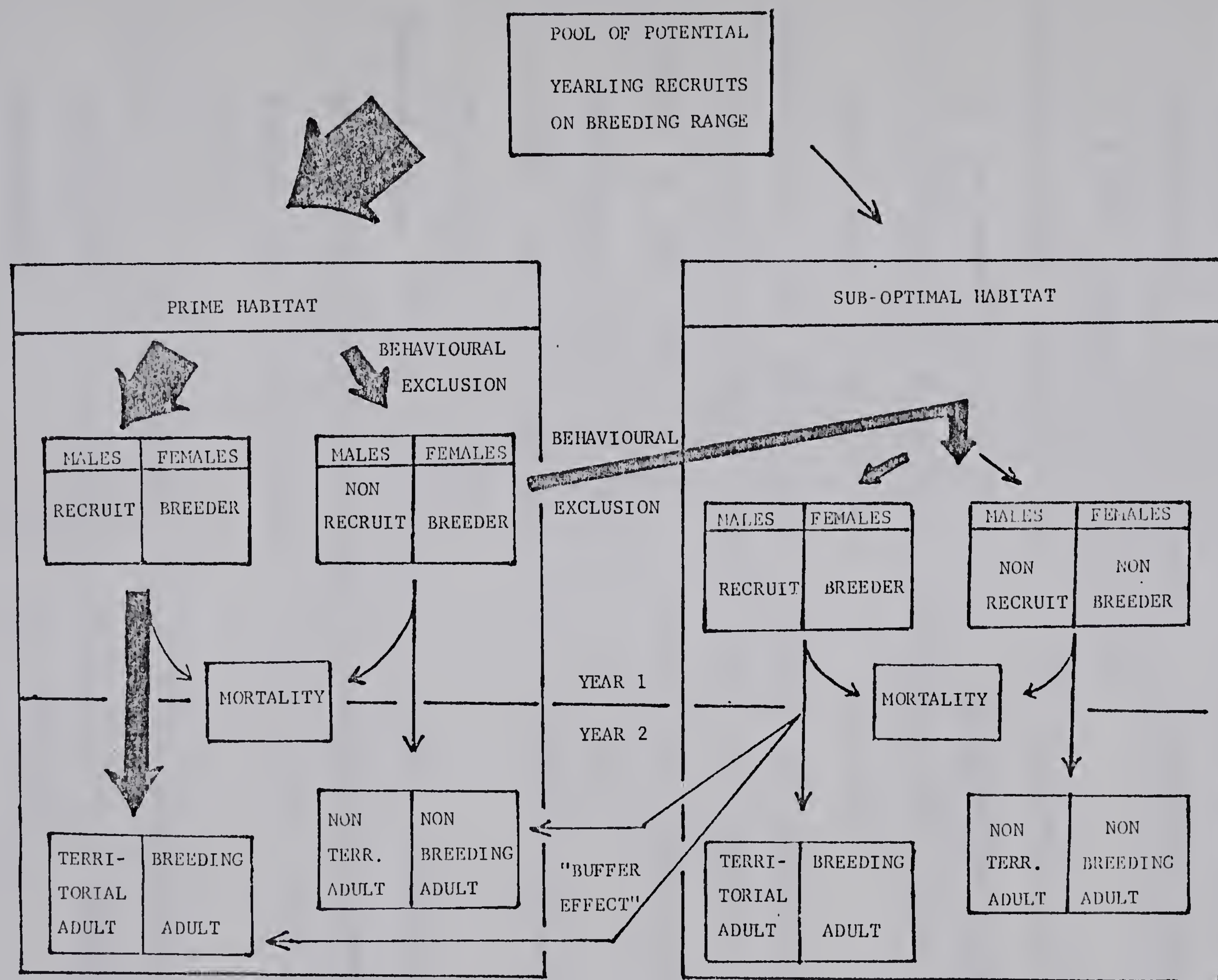

Figure 1. Options available to potential yearling recruits of both sexes present on prime habitat in early spring. Shaded arrows are proportional to the estimated number of yearlings entering each category.

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APPENDIX 1. Breeding Success and Nest Predation in Blue Grouse

Introduction

Factors influencing the susceptibility of nests or hens on nests to predation have rarely been examined in tetraonids, mainly because of the difficulty in finding nests (Johnsgard 1973). Also, we usually cannot identify the predator nor understand how they locate nests. I found nests of blue grouse (*Dendragapus obscurus fuliginosus*) by radio-tagging hens prior to nesting and then following them to their nests. Telemetry allowed the fate of nests to be monitored more efficiently than in the past. My objectives were to obtain an unbiased assessment of nesting success, to determine the fate of nests, and to see whether the fate was influenced by overhead concealment of nests, the age of the nest hen, timirg of nest initiation, and/or pre-nesting movements.

Study Area and Methods

This study was conducted on a 1200-ha area in the foothills of east-central Vancouver Island. Most nests were found on areas logged and/or burned less than 20 years ago. The area is described in detail by Zwickel (1975), Hannon (1978), and Sopuck (1978). All nests were found by monitoring hens by telemetry, commencing 2 to 4 weeks prior to nesting.

When a nest was found, the hen was flushed and the clutch size noted. A hen was disturbed in this manner only once, as occupancy of a nest was determined from 20-30 m by telemetry. Nest success was defined as the hatching of at least 1 egg. Time of abandonment of nests was determined within 1 to 4 days. Overhead concealment of nests was estimated using the following ratings: 1. poor- hen on nest easily visible. 2. moderate- hen on nest partially visible. 3. excellent- hen on nest not visible.

Predators of eggs or nest hens were identified using clues described by Einarsen (1956).

Except where specified, chi-square tests for independence or Student t-tests were used in statistical analyses. Mean values are presented plus or minus one standard deviation.

Results and Discussion

Information on 65 nests was obtained from 41 yearling and 16 adult females monitored in 1976 and 1977. Data for the 2 years were combined.

Forty-seven percent of all nests were successful (29/62, 3 nests that were deserted are excluded). This was lower than the 63% success of 142 nests found from 1963-1976 in the same area (Zwickel and Carveth 1978, $p<.05$). Since telemetry was not used in the latter sample, nests found at different stages of development were pooled. In contrast, all radio-tagged hens were monitored at the time of laying. This will result in the success rate reported by Zwickel and Carveth (1978) to be biased upwards (Miller and Johnson 1978) and may explain the difference in the 2 samples.

Success of nesting females, rather than of individual nests, was 52% (29/56). This apparent increase (not significant, $p>.05$) was due to 4 of 8 hens hatching second clutches. Six of these hens had their first nests destroyed by predators and 2 had deserted. Of 25 hens monitored with broods, 28% (7/25) lost their entire broods within 10 days of hatching. Thus, an estimate of the proportion of hens which successfully incubated a clutch and raised a brood to 10 days of age was 38% (21/56). Zwickel and Bendell (1967) found that most mortality of juveniles occurred within 2 weeks of hatching with generally high survival from then on.

Nesting success of adults (6/16) did not differ from that of yearlings (23/40, $p>.05$). Zwickel and Bendell

(1967), however, reported that adults had greater success than yearlings based on a higher proportion of adults with broods. They attributed the higher success to a higher rate of renesting in this age class, as found by Zwickel (1977), Hannon (1978), and Sopuck (1978). The relatively small sample of adults may have resulted in a low indicated success by chance, and since 3 adult hens were killed by predators and 2 were not monitored after losing their first clutches, more might have renested successfully.

Fate of nests was independent of the degree of overhead concealment at nest sites (Table 1, $p>.10$), although the trend was for increased success with greater concealment. A larger sample of 141 nests found from 1963 to 1976 in the same area (Table 2) indicated that the fates of nests were dependent on their concealment ($p<.01$) as well concealed nests had higher success than poorly concealed nests (63% versus 33%). Keppie and Herzog (1978) and Wallestad and Pyrah (1974), working on spruce grouse (*Canachites canadensis franklini*) and sage grouse (*Centrocercus urophasianus*), respectively, also found a relationship between nesting cover and nesting success. Higher success of adults may be related to selection of more concealed nest sites than yearlings, as reported by Keppie and Herzog (1978) for spruce grouse. However degree of nest concealment was independent of the age of the hen in my sample (Table 1, $p>.50$).

Timing of initiation may influence the fate of nests

because predators may develop a search image for nests after a peak in nesting occurs. This may be offset because new growth increases nesting cover later in the season. The median date of initiation of nests that were destroyed by predators (15 May) was not different than the date that successful nests were started (18 May, $p>.05$). This is an important consideration since adults began nesting earlier than yearlings (9 May versus 17 may, $p<.05$, renests excluded). However, advantages of earlier nesting may be that it allows more time for renesting, or allows juveniles more time on breeding range, thus increasing their survival.

I also considered, among yearlings, whether the extent of movement prior to nesting influenced nesting success. Wandering yearlings may be delayed in breeding (Sopuck 1978) and may select inferior nesting sites relative to localized yearlings. Nesting success of wandering yearlings (11/24) did not differ from that of localized yearlings (8/17,$p>.05$). However, 6 yearlings nested in sub-optimal habitat (Sopuck 1978). Of these, 2 hatched their eggs, but only 1 raised a brood to 10 days of age. In prime habitat (Sopuck 1978), 20 of 34 hens (59%) hatched eggs and 40% raised a brood to 10 days. Although samples are small, hens that nest in marginal areas may have lower breeding success.

The fate of unsuccessful nests was as follows: 78% (28/36) of all nesting failures were due to predation on eggs, 18% (5/36) were caused by the nest hen being killed, and 8% (3/36) were deserted. All 3 desertions occurred when

hens were flushed from nests during laying and were thought to be observer-caused, as concluded by Zwickel and Carveth (1978). Corvids were identified in 18% (5/28) of the cases where eggs were taken, in 2 nests (7%) eggs disappeared one by one; and in the remainder (75%, 21/28), no sign of eggs remained. Corvid predation is likely a minimal estimate because they may remove all eggshells from the nest. In 2 cases where eggs disappeared gradually, small mammalian predators such as red squirrels (*Tamiasciurus hudsonicus*) may have been responsible (F.C. Zwickel, pers. comm.). Where all eggs disappear suddenly, large mammalian predators, which devour all remnants of the eggs, may be responsible. There is unpublished evidence from an analysis of scats of black bear (*Ursus americanus*) that they may take a significant number of eggs of grouse in this area (Ray Prach, pers. comm.). Black bears are common on the study area. Avian predators such as Goshawks (*Accipiter gentilis*) and Golden eagles (*Aquila chrysaetos*) the most common large raptors in the area, killed 3 nest hens, while 2 were killed by mustelids, likely marten (*Martes americana*) and long-tailed weasel (*Mustela frenata*).

The probability of a nest remaining intact until the end of the laying period (about 8-10 days in blue grouse) was .95, until the end of early incubation (8 days after the completion of laying) .81, until the end of mid-incubation (17 days after laying) .63, and after late incubation (26 days after laying) .47. Again, samples are small, but nests

seem least susceptible to predation during laying. This may be because hens spend less time on their nests than during incubation, as reported by McCourt et al. (1973) for spruce grouse.

Since predators relying mainly on sight (ie. corvids) were identified in only 18% of egg losses, predators using both smell and sight (ie. bears, mustelids) may be most important in the destruction of clutches. Concealment of nests would tend not to inhibit the efficiency of scent location, although well concealed nests may be difficult to find once a hen is flushed. Corvids may have been more of a factor from 1963-1973, when plantations were small and available cover minimal. During 1976 and 1977, predators that hunt by scent may have had the major impact, hence lessening the advantage of well concealed nests, as found in my sample.

It should be emphasized that my sample was weighted heavily in favour of yearlings and hence did not reflect the actual age ratios in the population.

In summary, telemetry allowed a relatively large number of nests to be monitored, beginning at the same stage of development (laying) and providing an unbiased estimate of nest success. Following individuals through the reproductive period, provided an opportunity to determine the success of nesting females by accounting for renesting, and also an estimate of early brood survival.

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Work was conducted on lands of Crown Zellerbach Ltd., Courtenay Division.

Table 1. Fates of nests of radio-tagged hens in relation to degree of overhead concealment and the number of yearlings and adults nesting in each cover type, 1976 and 1977. Percentages are in parentheses.

	Concealment		
	Poor	Moderate	Excellent
Fates of nests:			
No. lost to predation	7 (70)	10 (53)	13 (43)
No. hatched	3 (30)	9 (47)	17 (57)
Total	10	19	30
Concealment of nests of:			
Adults	4 (21)	5 (26)	10 (53)
Yearlings	7 (16)	14 (32)	23 (53)

Table 2. Fates of nests of non-radio-tagged hens in relation to degree of overhead concealment, 1963-1976. Percentages are in parentheses.

	Concealment		
	Poor	Moderate	Excellent
Fates of nests:			
No. lost to predation	11(65)	12(32)	28(32)
No. hatched	6(35)	25(68)	59(68)
Total	17(12)	37(26)	87(62)

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APPENDIX 2. Renesting By Adult and Yearling Blue Grouse

About 40% of nests of blue grouse (*Dendragapus obscurus*) found in 10 years of study of a population on Vancouver Island were destroyed by predators (Zwickel and Carveth 1978). Thus, data on the ability of hens to renest is important in determining the number and age of hens successfully bringing off broods. Information on renesting in blue grouse has been obtained from observations of individually marked birds (Zwickel and Lance 1965), occurrence of late hatched broods (Zwickel 1977), and analysis of post-ovulatory follicles (Hannon 1978). Only 1 case of renesting was confirmed by field observations where first and second nests were found (Zwickel and Lance 1965). My observations of 8 radio-tagged hens that renested provide an opportunity to investigate this phenomenon in more detail.

During May and June of 1976 and 1977, movements of 25 yearling and 6 adult hens were monitored during and after abandonment of their first clutches. Of these, a higher ($p<.05$) proportion of adults renested (83%, 5/6) than yearlings (12%, 3/25).

The difference between adults and yearlings is supported by other data. Hannon (1978) reported that 5 of 12 (42%) adults in which post-ovulatory follicles could be counted had renested, whereas only 1 of 13 (8%) yearlings had done so. Zwickel (1977) indicated that most late-hatched broods probably are a result of renesting. He found that

adults had more late broods that yearlings, but did not give the proportions of each.

Fifty percent of the clutches in second nests hatched (4/8), a figure similar to the 45% success of all first nests of radio-tagged hens (Sopuck 1978, n=56). This is an important statistic; it means that about 1/2 of the hens which lose first clutches, but renest will bring off broods. This was also shown by Errington and Hamerstrom (1937) for pheasants (*Phasianus colchicus*).

On average, hens nested the second time 206±183 m (range: 40-620) from first nests and occupied an area of 3.5±3.4 ha (range: 0.9-11.0 ha) during the renesting interval. The large standard errors were due to one bird, a yearling, that nested 620 m from her first nest and occupied an area twice as large as any other hen. In general, hens appear to be remaining on their pre-nesting home ranges in their search for suitable renesting sites.

Six hens with second nests lost first clutches to predators and 2 deserted. Two abandoned first nests when laying, 3 during early incubation (1-8 days after completion of laying), 2 during mid-incubation (9-17 days), and 1 during late incubation (18-26 days). The incubation period is about 26 days in blue grouse (Zwickel 1977). The average time for hens to initiate second nests was 13±2 days (range: 9-15 days). The hen that renested after 9 days lost her first clutch to a predator during early incubation, while

the hen that renested after 15 days lost her first clutch after 18 days of incubation. This suggests that the length of time required to renest may increase with the stage of incubation when loss occurs. Gates (1966) thought regression of ovaries was responsible for this phenomenon in pheasants. Another factor may be the loss of body weight of hens as incubation proceeds (Redfield 1973, Zwickel and Carveth 1978). Three of 4 adults that lost nests during mid- to late incubation renested, while none of 11 yearlings did so. Thus, higher weights of adults (Redfield 1973, Zwickel and Carveth 1978) than yearlings at the start of incubation may increase their capacity to renest.

Average size of clutch in second nests of adults (5.25±.50) may be higher than that of second nests of yearlings (4.67±.58), although the difference was not significant. Average size of second clutches of all females (5.00±.58) was lower than that of first clutches (5.82 ±1.07, n=45, Sopuck 1978), but the difference also was not significant (.05<p<.10).

Zwickel (1975) found that clutches of adults hatched after 30 June were smaller than those hatched before this date and concluded that second clutches were smaller than first. My data show that the mean date of hatch of second nests was 11 July±4 days (range: 5 July-17 July, n=8), while the mean date of hatch of first nests was 20 June ±7days (range: 9 June-5 July n=42) for yearlings and 13 June±5 days (range: 6 June-19 June, n=16) for adults. Thus, the 30 June

cut-off date used by Zwickel (1975) for first nests of adults seems valid. Since 7% (3/42) of yearlings hatched first nests after 30 June, 5 July may be a suitable cut-off date for yearlings.

My data indicate that adults have a higher rate of renesting than yearlings. If adults hatch about 1/2 of their second nests they should be more successful than yearlings in bringing off broods. This assumption is supported by field data as Zwickel and Bendell (1967) reported that a higher proportion of adults have broods than yearlings. This difference in reproductive potential between adults and yearlings means that success of first clutches of yearlings may be a major factor causing variation in productivity among years. This was also suggested by Wallestad (1975) for sage grouse (Centrocercus urophasianus). When nesting success is low, yearlings in general will do poorly (adults will be less affected); resulting in low productivity. If nesting success is high, both yearlings and adults will do well, resulting in high productivity in that year.

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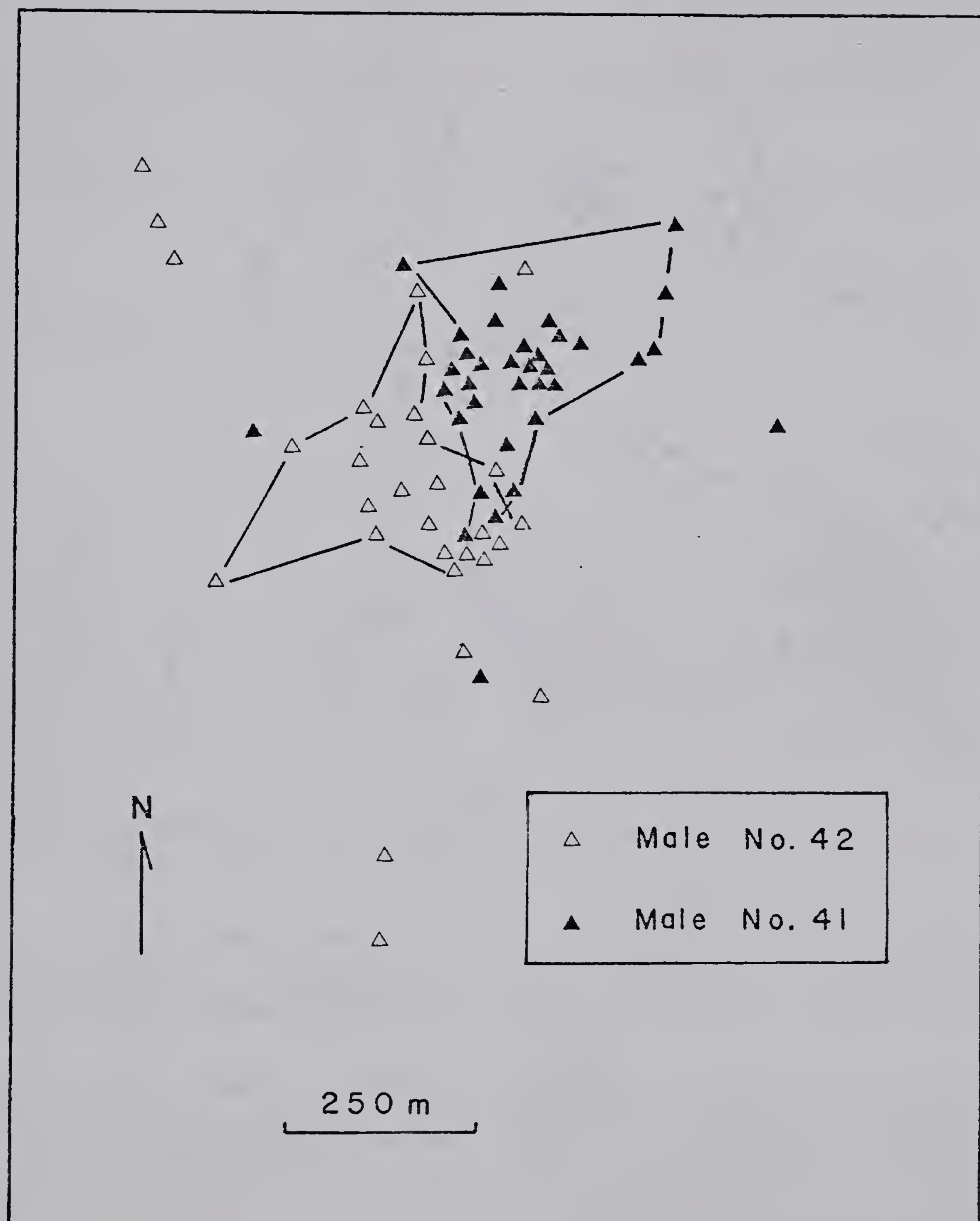
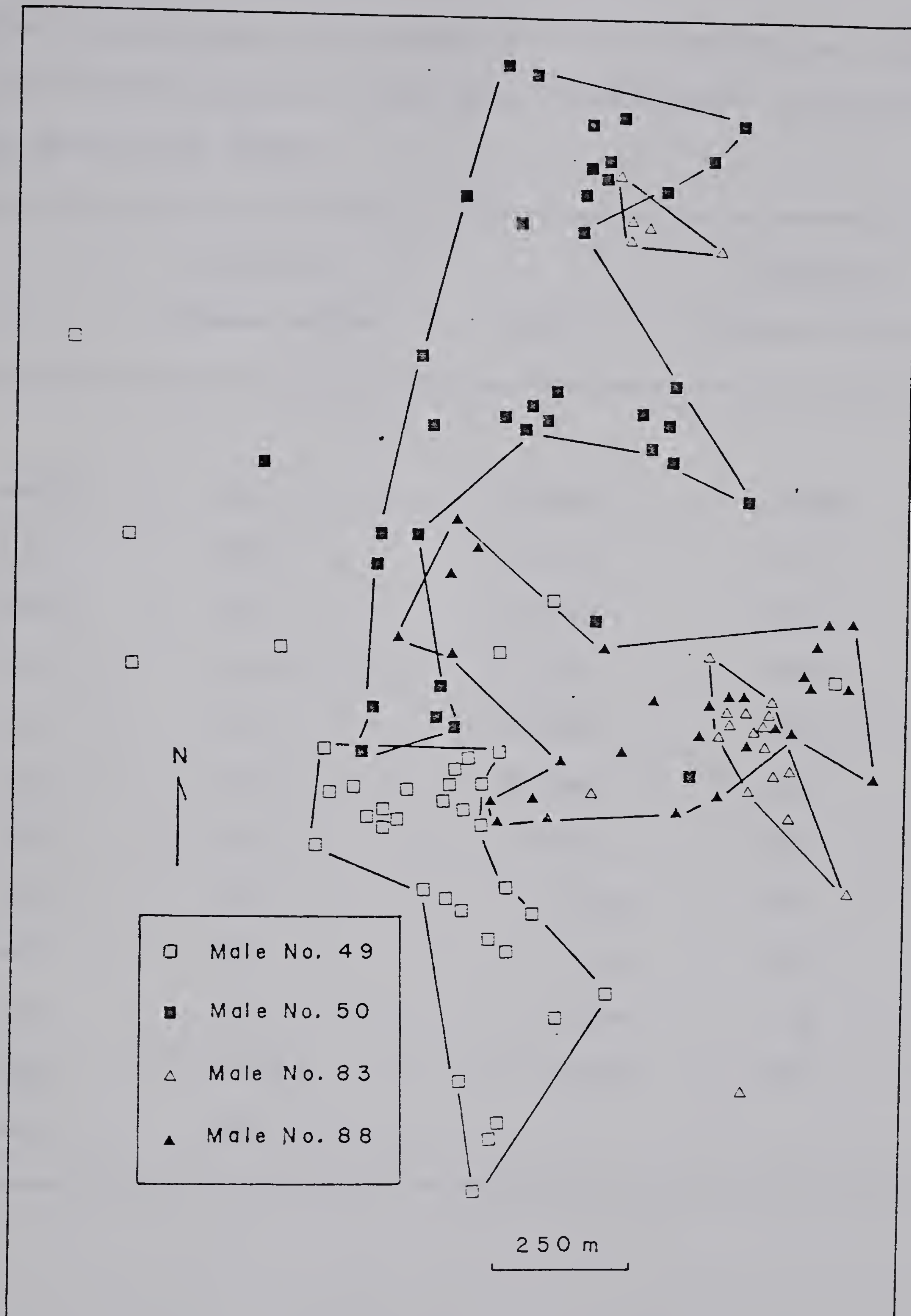
APPENDIX 3. Spatial Relationships of Yearling Males Occupying Adjacent Areas

The activity centres of males No. 41 and 42 were essentially separate from April to June (Figure 1), with only a slight degree of overlap. The activity centres of Males No. 49 and 50 also were largely separate from males No. 83 and 88 (Figure 2). However, considerable overlap in the home ranges of males No. 83 and 88 occurred during the recruitment period. These males were located approximately during the same time each day and the distance between these birds on each day is given in Table 1. In only 4 cases were these two males within 100 m of each other indicating they were separated temporally rather than spatially.



Appendix 3, figure 1. Radio-locations of 2 yearling males occupying adjacent areas from April to june, 1977. Core areas of use are delineated.



Appendix 3, figure 2. Radio-locations of 4 yearling males occupying adjacent areas, April to June, 1977. Core areas of use are delineated.

Table 1. Distances (m) between spatially overlapping males No. 83 and 88 during 23 days where simultaneous locations of both males were made.

Date	Distance between males	Date	Distance between males
16 April	620	18 May	1080
18 April	750	20 May	230
20 April	740	24 May	600
25 April	1160	25 May	620
1 May	230	28 May	360
4 May	140	30 May	380
6 May	400	31 May	90
9 May	180	1 June	30
10 May	90	2 June	240
12 May	260	3 June	110
14 May	1020	6 June	80
16 May	860		